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A SURVEY OF THE ARTHROPOD SOIL AND LITTER FAUNA OF SOME FOREST RESERVES AND CACAO ESTATES IN TRINIDAD, BRITISH WEST INDIES

BY A. H. STRICKLAND

(With 1 Figure in the Text)

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1. INTRODUCTION

Apart from the investigations of Beebe (1916) in Brazil, Dammerman (1925, 1937) in the Dutch East Indies, Van Zwaluwenburg (1931) in Hawaii, Berwick (1934–5) in Trinidad, and Williams (1942) in Panama, virtually no work appears to have been done on the arthropod fauna of soil and surface litter in the tropics. This seems to be due largely to lack of enthusiastic workers, the difficulty of obtaining a quantitative estimate of the animals in a sample of soil, and the virtual impossibility of obtaining anything better than determinations to family or generic status of most of the material encountered. The last of these objections can only be overcome by widespread collecting of soil fauna all over the tropics and submitting the collections to specialists in the groups concerned. It is for this reason that much of the material collected in the present investigation has been placed in the hands of various specialists for description as soon as conditions permit.

2. METHODS

(*a*) *Sampling*

A core auger of internal diameter 3·6 in. was used to take all the samples. Sampling methods were as follows:

(1) The area to be sampled was surveyed on arrival and a plot was selected, large enough to cover all the major local variations in vegetation and soil type and surrounded on all sides by the same type of vegetation and soil. In practice, the area of the plots varied between 400 and 2000 sq.yd., according to the typicalness of the area as a whole.

(2) Five sampling stations were set at random, one in each fifth of the plot, and each plot—with one exception—was sampled twice, once to a depth of 9 in., and the second time to a depth of 3 in. The surface litter was first removed and placed in a tin. The soil samples were then taken in the form of cores 3·6 in. in diameter and 3 in. in length. Each 'sample' referred to in the following pages hence consists of five 3·6 in. diameter cores. To convert the population of any sample into the conventional 'millions per acre', the number of animals should be multiplied by 0·125.

(3) A composite soil sample for chemical analysis was taken from each plot. This consisted of a sliver of soil from the side of each auger hole.

(4) Notes were taken before departing of the state of the soil, vegetation, and average thickness of the surface litter.

In order to test the suitability of these sampling methods, two series of five samples each were taken to a depth of $1\frac{1}{2}$ in. on a plot of area 1600 sq.yd. at Tortuga estate. The samples in each series were extracted individually and analysed statistically. Series A gave a population of 63·12, and series B a population of 54·92 millions per acre. For the two series to show a significant difference at the 5% point, 'D' would have to be greater than 26·57 millions per acre. The actual difference of 8·20 millions per acre is therefore not significant, and can be attributed to the normal errors of random sampling.

(*b*) *Extracting the samples*

A modified flotation process was used to extract the fauna from the samples. On returning to the laboratory the soil samples—unless of fine sand—were placed in individual glass jars of half saturated NaCl solution and allowed to deflocculate. After a

20–24 hr. soak, the sample was placed in the extraction apparatus (Fig. 1), on the 0·1 mm. sieve, and covered with the salt solution, remaining in the deflocculating jar. The jar was washed out with fresh salt solution, which was likewise poured into the apparatus. The air compressor (a 'Dymax' aquarium blower of 1/150 h.p. rating) was switched on, and fine bubbles allowed to percolate the soil-salt solution mixture for 5–10 min. The process disentangled the arthropod fauna and vegetable debris from the soil and carried them to the surface of the solution. The compressor was switched off, and most of the sediment allowed to settle. More salt solution was then added from the aspirator, sweeping the vegetation and fauna over the lip and on to a double thickness of 1/100 in. mesh muslin held by an elastic band on to a glass cylinder. The used salt solution was carried away to a settling tank via the filter funnel supporting

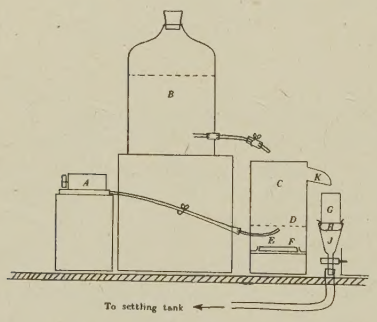

Fig. 1. The extraction apparatus. *A* = 'Dymax' air compressor. *B* = NaCl reservoir. *C* = extraction apparatus constructed out of two 2 gal. paint tins. The sieve *D* was soldered to the base of one paint tin (from which the bottom had been cut out). The second tin was cut in half and the top half, with the lid *F*, was soldered to the bottom of the whole pot. A metal tube *E* was drawn to a fine point at one end and soldered into the side of the lower half-paint tin. A lip *K* was constructed and soldered an inch below the top of the whole pot. It should be noted that the lid *F* was watertight and easily removable for cleaning purposes. *G* = glass cylinder with muslin *H* held on to its lower end with an elastic band. *J* = filter funnel supporting the glass cylinder, and conducting used salt solution to the settling tank.

the glass cylinder. The material on the muslin was carefully washed into a beaker with tap water, and brought to the boil (this served the dual purpose of killing the fauna in an extended state, and driving the air out of the vegetation, causing it to sink to the bottom of the beaker). On cooling, 15–20 c.c. of kerosene were added, and the contents well stirred. All those animals with chitinous exoskeletons were taken up by the kerosene layer, and could easily be decanted off on to a double thickness of muslin practically free from contamination. The muslin was stretched taut over a 6 × 4 in. photographic plate, and the animals could be picked off with ease under a low power binocular microscope. In practice it was found advisable to give 3–4 treatments with kerosene if much vegetation was present, as small mites tended to adhere to the rotting leaves and could not be detached without considerable shaking.

The soil residue from each sample examined was washed into a residue can. When a series under examination was complete, the contents of the can were covered with salt solution and well stirred. The sediment was allowed to settle, and the salt solution filtered. By this means it was demonstrated that approximately 95 % of the fauna was extracted from the samples in the initial process. All the quantitative results in this paper include these residue counts. Surface litter was extracted simply by boiling, cooling, and treating with kerosene.

The time taken from removing a 3 in. sample from the deflocculating jar to the extraction apparatus and placing the last animal in its specimen tube naturally varied with the population of the sample. On the average, a 0–3 in. sample containing about 300 individuals took 1½ hr. It should be remembered, however, that during the bubbling and boiling processes the operator can be busying himself counting the animals in the previous sample, and so in practice the time spent per sample is more in the region of 50 min. to 1 hr.—including washing out the apparatus ready for the next sample.

3. THE AREAS SAMPLED

It was originally intended that an equal number of cacao estates and forest reserves should be sampled regularly over the six months rainy season of 1943. Restrictions on the author's time and on motor transport prevented the completion of this scheme, and a modified sampling plan had to be evolved. This included two sampling trips to each of seven areas described in Table 1—three forest reserves, and four cacao estates. The soil constants (index of texture, normal *p*H, organic matter % and carbon/nitrogen ratio) are the mean figures obtained from the analyses of two composite samples taken as described in § 2 (*a*) (2). The presence or absence of white fungus sheet mycelium in the surface litter has been stressed in view of the numbers of fungivorous springtails, beetles and larval Diptera encountered at Matura reserve and Las Hermanas and Tortuga estates.

Table 2 gives the population figures for the two series of samples taken in each area. These results are discussed at some length in § 4 (*c*), as are the data shown in Check List 1.

The majority of the insect and other arthropod material collected in the course of this investigation has been deposited in the Department of Entomology at the Imperial College of Tropical Agriculture in Trinidad. Although partly named examples of most of the ants encountered are also at the Imperial

Table 1. *The areas sampled*

Area	Vegetation: Species	Vegetation: Dominant in story	Surface litter: Mean thickness (in.)	Surface litter: Remarks	Soil: Type	Soil: Index of texture	Soil: *p*H	Soil: % organic matter	Soil: Carbon/nitrogen ratio	Samples: Date (1943)	Samples: Depth (in.)	Remarks
A. Forest Reserves												
1. Tumpuna Reserve	*Carapa guianensis* Aubl.* *Eschweilera subglandulosa* Miers *Maximiliana elegans* Karst *Pentaclethra macroloba* (Willd.) Kuntze	Emergent Canopy Lower	1–2½	White fungus mycelium, patchy in distribution	Heavy clay	35–40	5·8	6·0	8·2	23 July 18 Sept.	Litter 0·3, 3·6, 6·9 Litter 0·3	Area of plot = 1600 sq.yd.: mostly on a slope of 1 in 12. Very little erosion owing to accumulation of organic matter in soil 'crumb' layer
2. Arena Reserve	Same as above, save that on second plot sampled there was a profuse growth of: *Ischnosiphon arouma* (Aubl.)	Lower Bottom	1–2	Fungus not so abundant as at Tumpuna	Light quartzose sand	4	4·9	3·4	13·7	23 July 18 Sept.	Litter 0·3, 3·9, 9·15 Litter 0·3	Area of first plot = 750 sq.yd. of second = 600 sq. yd. Both plots on level ground. No erosion
3. Matura Reserve	*Mora excelsa* Bth. *Carapa guianensis* Aubl. *Eschweilera subglandulosa* (Steud) Miers *Licania biglandulosa* Griseb. *Cassipourea latifolia* Alston	Canopy (88 %) (8 %) (4 %) Middle Lower	3 (1½–6)	Many *Mora* nodules present in samples. Fungus not conspicuous	Detrital silt with much sand	5	3·9	3·0	22·0	8 July	Litter 0·3, 3·6, 6·9	Low-lying rain forest with a high water table producing swampy conditions. Area of plot = 150 sq.yd. Sampling impeded by boggy nature of ground and profusion of young *Mora* saplings
B. Cacao Estates												
1. Brigand Hill Estate	*Erythrina micropteryx* Poepp. ex Walp. *Theobroma cacao* L. *Urticaria* spp. *Commelina* sp.	Canopy (shade trees) Middle (crop) Ground cover (weeds)	½–1	Litter very sparse. Fungus absent	Heavy clay	52	5·8	5·8	10·5	9 Aug. 10 Sept.	Litter 0·3, 3·6, 6·9 Litter 0·3	Area of plot = 440 sq.yd. Some erosion due to torrential rain at first visit. As a result, many cacao rootlets were showing through the leaf mat on the second visit
2. Tortuga Estate	As above, save that a thick mat of *Zebrina pendula* Schnizl. formed the dominant ground cover	Do.	¾	Fungus very conspicuous and widely distributed	'Chocolate' clay-loam	48	6·5	5·8	10·5	22 June 30 Aug.	Litter 0·3, 3·6, 6·9 Litter 0·3	Area of first plot = 1600 sq.yd., of second = 2000 sq.yd. In spite of torrential rains the surface crumb structure of the chocolate soil maintained itself in a characteristically remarkable manner
3. Las Hermanas Estate	As above, with the addition of an undetermined weed of the genus *Piper*	Do.	1–2	Do.	Silty clay	43	4·8	4·0	8·5	9 Aug.	(1) Litter 0·3, 3·6, 6·9 (2) Litter 0·3	Area of plot = 2000 sq.yd. Surface root mat very conspicuous, indicating that the soil was not a good one for easy root penetration
4. River Estate	As above, but several species of grassy weeds and ferns competing for dominance. Weeds in general patchy in distribution	Do.	½–2	Fungus present where litter over 1½ in. thick, otherwise absent	Sandy detrital silt	13	6·8	3·5	8·8	4 Sept.	(1) Litter 0·3, 3·6, 6·9 (2) Litter 0·3	Area of plot = 750 sq.yd. Four out of the ten samples were taken on weedy areas

* 'Crappo-Guatecare-Cocorite' Association.

Table 2. *Population figures for the areas sampled*

Groups	Tumpuna Reserve							Arena Reserve							Matura Reserve				
	L	0–3	3–6	6–9	L	0–3	Total	L	0–3	3–9	9–15	L	0–3	Total	L	0–3	3–6	6–9	Total
Isopoda	2	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—
Arachnida (not Acarina)	4	3	2	—	2	1	12	2	—	2	—	1	4	9	1	—	—	1	2
Acarina	582	158	70	18	137	232	1197	273	203	82	43	357	268	1226	490	316	64	44	914
Myriapoda	5	3	1	1	3	1	14	1	6	3	2	24	4	40	7	—	—	—	7
Thysanura	—	—	3	—	—	—	3	—	—	—	—	—	1	1	2	—	1	—	3
Collembola	10	2	—	—	1	2	15	—	—	—	—	22	8	30	14	—	—	—	14
Orthoptera	14	—	1	—	—	—	15	—	1	—	—	—	—	1	—	—	—	—	—
Isoptera	6	—	—	—	2	591	599	46	75	12	5	55	36	229	10	58	3	—	71
Thysanoptera	—	—	—	—	3	3	6	—	—	—	—	—	—	—	—	1	—	—	1
Hemiptera	6	3	—	—	1	37	47	2	—	1	—	4	3	10	12	3	11	—	26
Dermaptera	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Coleoptera, larvae	5	2	3	1	—	4	15	3	3	1	—	—	1	8	8	2	4	—	14
Coleoptera, adults	4	2	—	—	—	11	17	1	—	—	—	1	4	6	2	3	—	1	6
Diptera, larvae	39	16	16	—	—	10	81	9	12	3	4	9	4	41	26	6	2	—	34
Diptera, adults	3	4	2	—	3	—	12	—	3	—	—	1	—	4	1	1	1	—	3
Lepidoptera, larvae	—	1	1	—	—	—	2	1	—	—	—	2	—	3	1	—	—	—	1
Formicidae, larvae	1	—	—	—	2	4	7	1	—	—	—	27	4	32	7	—	3	—	10
Formicidae, adults	14	7	—	—	7	83	111	35	95	9	3	87	45	274	27	22	18	4	71
Other Hymenoptera	3	—	—	2	—	1	6	—	2	—	—	1	—	3	5	2	—	2	9
Undetermined larvae	2	3	—	—	2	4	11	—	1	—	1	1	1	4	—	—	—	—	—
Totals	700	204	99	22	163	984	2172	374	401	113	58	592	383	1921	613	414	107	52	1186

Groups	Brigand Hill Estate							Tortuga Estate							Las Hermanas Estate							River Estate							Grand total
	L	0–3	3–6	6–9	L	0–3	Total	L	0–3	3–6	6–9	L	0–3	Total	L	0–3	3–6	6–9	L	0–3	Total	L	0–3	3–6	6–9	L	0–3	Total	
Isopoda	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1	—	1	4
Arachnida (not Acarina)	3	1	—	—	—	2	6	1	6	2	1	4	27	41	1	6	2	2	5	3	19	—	1	—	—	1	1	3	92
Acarina	118	125	42	20	60	96	461	198	93	23	19	172	119	624	594	229	91	37	431	298	1680	167	157	15	7	238	166	750	6,852
Myriapoda	3	2	—	1	3	3	12	—	1	—	—	—	—	1	6	2	—	—	4	4	16	1	—	—	—	3	3	7	97
Thysanura	—	1	—	1	—	—	2	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	1	—	—	—	—	1	11
Collembola	2	—	—	2	—	—	4	26	11	5	4	35	17	98	4	6	5	—	6	1	22	15	1	2	1	14	4	37	220
Orthoptera	—	—	—	—	—	—	—	—	—	2	—	—	—	2	—	—	—	—	—	1	1	1	—	—	—	1	—	2	21
Isoptera	—	1	2	2	6	76	87	—	—	—	—	—	—	—	1	5	—	—	17	—	23	—	—	—	—	4	37	41	1,050
Hemiptera	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7
Dermaptera	1	10	1	1	1	9	23	3	2	1	2	3	3	14	6	26	5	—	109	84	230	4	16	4	—	3	—	27	377
Coleoptera, larvae	—	—	—	—	—	1	1	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1	1	3
Coleoptera, adults	—	3	4	3	—	2	12	4	3	—	1	4	5	17	7	9	1	—	14	9	40	3	3	5	1	6	1	19	125
Diptera, larvae	3	3	2	2	2	10	22	3	2	—	—	3	2	10	5	2	5	—	17	7	36	1	—	1	—	10	—	12	99
Diptera, adults	1	—	3	1	3	—	8	10	3	—	1	8	3	25	5	8	5	—	18	42	78	25	15	1	—	16	2	59	326
Lepidoptera, larvae	7	3	1	2	3	2	18	8	7	2	1	1	14	33	20	3	3	—	3	7	36	5	8	—	—	1	—	14	120
Formicidae, larvae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	2	8
Formicidae, adults	1	3	—	—	—	—	4	—	—	—	—	—	1	1	—	2	—	3	1	1	7	—	11	—	—	2	5	18	78
Other Hymenoptera	5	95	40	22	2	110	274	3	31	32	12	1	34	113	—	62	20	16	33	86	217	6	176	53	26	35	160	456	1,516
Undetermined larvae	3	—	7	—	2	1	13	5	2	2	2	8	3	22	5	2	2	—	2	—	11	2	3	—	—	—	—	5	69
Totals	—	4	—	—	2	1	7	—	1	3	—	—	—	4	4	1	—	—	8	4	17	8	—	—	—	2	—	10	53
	147	251	102	57	84	313	954	262	162	73	43	239	228	1007	658	363	139	58	669	547	2434	238	392	81	35	338	381	1465	11,128

(L=litter; 0–3, etc. are depths of sample in inches.)

Check List 1. *Distribution of arthropod groups*

		Tum-puna	Arena	Matura	Brigand Hill	Tortuga	Las Her-manas	River
INSECTA								
HYMENOPTERA	Apoidea	.	.	.	.	×	.	.
	Chalcidoidea	.	.	.	×	.	.	.
	Cynipoidea	.	.	.	×	.	.	.
	Ichneumonoidea	.	.	.	.	.	×	.
	Parasitica indet.	.	.	.	×	.	×	×
	Proctotrypoidea	×	×	×	×	.	.	.
	Vespoidea	×	.	.	.	×	×	.
	Formicoidea	×	×	×	×	×	×	×
COLEOPTERA	Bostrichidae	×	.	×	×	.	×	.
	Cantharidae	.	.	.	.	×	×	.
	Carabidae	×	×	.	×	×	×	×
	Chrysomelidae	.	.	.	.	.	×	×
	Colydiidae	.	.	.	.	×	×	.
	Cucujidae	.	.	.	×	×	.	.
	Curculionidae	×	.	×	.	.	.	×
	Cryptophagidae	.	.	.	×	.	.	.
	Elateridae	.	×	.	×	.	×	×
	Lyctidae	.	.	.	.	×	.	.
	Lymexylonidae	×	.	.	.	.	.	.
	Ptiliidae	×	×	.	×	×	×	×
	Ptilodactylidae	×	.	.	.	.	.	×
	Scarabaeidae	.	.	.	.	×	.	.
	Scolytidae	×	.	×	.	.	×	.
	Scydmaenidae	.	×	.	×	.	.	.
	Staphylinidae	×	×	×	×	×	×	×
	Tenebrionidae	×	×	.	×	×	×	×
DIPTERA	Agromyzidae	.	.	.	.	×	.	.
	Borboridae	.	.	.	×	.	.	.
	Cecidomyidae	×	.	×	×	×	×	.
	Chironomidae	×	.	.	×	×	.	.
	Culicidae	.	.	.	×	×	.	.
	Dolichopodidae	.	.	.	.	.	.	×
	Fungivoridae	×	×	×	×	×	×	×
	Heleidae	×	.	.	×	×	×	.
	Ortalidae	×	.	.	.	.	.	.
	Phoridae	×	×	.	×	.	.	.
	Psychodidae	×	.	×	×	×	×	×
	Scatopsidae	×	.	.	.	×	.	.
	Stratiomyidae	.	×	.	.	.	.	.
	Nematocera, larvae	×	×	×	×	×	×	×
LEPIDOPTERA	Larvae indet.	×	×	×	.	.	.	×
HEMIPTERA	Berytidae	.	× ?	.	.	.	×	.
	Capsidae	×	×	.	×	×	×	×
	Cercopidae	.	×	.	×	×	×	×
	Coccidae	×	×	×	×	.	×	×
	Cryptostemmatidae	×	×	.	.	×	×	.
	Psyllidae	.	×	.	.	.	.	.
	Heteroptera nymphs	.	.	×	×	.	.	.
ORTHOPTERA	Acridiidae	×	.	.	.	.	×	.
	Blattidae	.	.	.	.	×	.	×
	Gryllidae	×	×	.	.	.	.	×
ISOPTERA	Kalotermitidae	.	.	×	.	.	.	.
	Termitidae	×	×	.	×	.	×	×
DERMAPTERA	Forficuloidea	.	.	.	×	×	.	×
THYSANOPTERA	Families indet.	×	.	×	.	.	.	
THYSANURA	Japygidae	×	×	×	×	×	×	×
COLLEMBOLA	Families indet.	×	×	×	×	×	×	×

Check List 1 (*continued*)

		Tumpuna	Arena	Matura	Brigand Hill	Tortuga	Las Hermanas	River
ARACHNIDA								
Araneae	Families indet.	×	×	×	×	×	×	×
Chelonithida	Families indet.	×	×	.	.	×	×	.
Acarina	Acaridae	×	×	×	×	×	×	×
	Galumnidae	×	×	×	×	×	×	×
	Haplodermatidae	×	×	×	×	×	×	×
	Nothridae	×	×	×	×	×	×	×
	Oribatoidea other than Galumnidae	×	×	×	×	×	×	×
	Parasitidae	×	×	×	×	×	×	×
	Uropodidae	×	×	×	×	×	×	×
	Other families indet.	×	×	×	×	×	×	×
MYRIAPODA								
Chilognatha	Julidae	.	×	.	×	×	×	.
Chilopoda	Geophilidae	×	×	×	×	.	.	.
	Lithobiidae	.	.	×	×	.	.	×
	Scolopendridae	.	.	.	.	.	×	×
Diplopoda	Polydesmidae	×	×	×	×	.	×	×
Symphyla	*Scutigerella*	.	.	×	×	.	×	×
CRUSTACEA								
Isopoda	Oniscidae	×	.	.	.	×	.	×

College, the complete collection of these insects is in the hands of Dr Neal A. Weber, of the University of North Dakota, U.S.A., for description as soon as conditions allow. Apart from the exceptions mentioned in the acknowledgements at the end of this paper, all of the family identifications were made by the author.

4. DISCUSSION OF RESULTS

It was unfortunate that the original list of comparable cacao and forest areas that had been scheduled for sampling had to be very much curtailed. Those areas that were sampled do, however, form a basis for comparing the arthropod soil fauna of primary rain forest, untouched by the hand of man, and a plantation crop, where man's hands (and, of especial importance in the present case, his feet), are ever present, under varying pedological conditions. In brief, the areas may be compared as follows:

Tumpuna Reserve, Arena Reserve	Heavy clay, Light sand	Same consociation
Matura Reserve, River Estate	Detrital silt	Forest, Cacao
Tumpuna Reserve, Brigand Hill Estate	Heavy clay	Forest, Cacao
Tortuga Estate, Brigand Hill Estate, Las Hermanas Estate	All clays or Silty clays	Fine cacao, Good cacao, Poor cacao

Again, largely owing to restrictions on time, it was found impossible adequately to assess and identify many of the species and genera encountered in the various samples. Five genera of ants, and five genera of mites—selected from the most commonly occurring forms—were, however, estimated apart from the main bulk of these groups and these results, along with Check Lists of the partly identified ants and mites, are given below.

(*a*) *The ant fauna*

Check List 2 gives the generic determinations (made by Dr Neal A. Weber) of the ants taken in the areas sampled. It is of interest to note the predominance (12 genera) of Myrmecine ants. The majority of the members of this subfamily are carnivorous, but many species are of more direct economic importance as leaf-cutters—it will be seen that at least seven species of the tribe Attini are represented in the list. The Ponerinae are the next most common subfamily, contributing seven genera and at least fourteen species to the list. The Formicinae, although only represented by three genera, are of interest in view of the widespread distribution of the genus *Rhizomyrma*. This genus is of considerable economic importance since some if not most of its members are obligatory coccid farmers (Bünzli, 1935; Weber, 1944). In one series of samples taken at River Estate (not included in the present paper) and in a second series taken at Las Hermanas Estate, Table 3 shows the figures obtained, which suggest that *Rhizomyrma* spp. are actively engaged in tending coccids—*Rhizoecus moruliferus* Green and *Ortheziopa* sp.—on cacao roots in Trinidad.

The presence of a single species of the predominantly Old World genus *Cerapachys* is interesting, in so far as Wheeler (1922) states: 'It seems hardly

possible that species of *Cerapachys, sensu latiore,* are entirely lacking in South America, but none has been found in any of the many extensive collections that have been made on that Continent' (p. 53).

Table 3. *Ant: coccid populations*

	River Estate		Las Hermanas Estate	
	Litter	0–2 in. soil	Litter	0–3 in. soil
Rhizomyrma spp.	3	133	2	105
Coccidae	3	167	59	83

In all, 23 genera and at least 56 species of ants were taken from the samples of litter and soil examined in the present investigation.

Check List 2. *Ants taken from soil and litter samples*

CERAPACHYINAE	Cerapachini	*Cerapachys* sp.
PONERINAE	Amblyoponini	*Stigmatomma* sp.
	Ectatominini	*Prionopelta* sp.
		Gnamptogenys, 2 spp.
	Proceratiini	*Discothyrea*, 1 sp.?
	Ponerini	*Pachycondyla* sp.
		Ponera trigona Forel
		Ponera, 4 spp.
	Odontomachini	*Anochetus inermis* Mayr
		Anochetus, 2 spp.
MYRMECINAE	Pheidolini	*Pheidole*, 5 spp.
	Solenopsidini	*Solenopsis*, 11 spp.?
		Monomorium (floricola?)
		Monomorium sp.
	Myrmecinini	*Myrmecina* sp.?
	Leptothoracini	*Rogeria* sp.
	Ochetomyrmicini	*Wasmannia*, 4 spp.
	Dacetonini	*Basiceros* sp.?
		Rhopalothrix sp.
		Strumigenys sp.
	Attini	*Myrmecocrypta buenzlii* Borgmeier
		Myrmecocrypta, 2 spp.
		Mycocepurus smithii Forel
		Mycocepurus, 2 spp.
		Sericomyrmex urichi Forel
FORMICINAE	Plagiolepidini	*Rhizomyrma*, 4 spp.
	Myrmelachistini	*Brachymyrmex*, 2 spp.
	Prenolepidini	*Nylanderia* sp.?

Table 4 gives the quantitative results of the five genera of ants that were estimated separately. It should be noted that possibly more than four species are represented in the *Solenopsis* column, but if this is the case it will not upset the validity of the figures since only the four species were commonly encountered in large numbers, other species being found singly or in twos and threes. *Solenopsis* spp. are undoubtedly the most widely and commonly distributed soil ants in the areas sampled. Of the next commonest ants—*Rhizomyrma* spp.—just over half the number of individuals were taken, and these were not so widely distributed as the *Solenopsis* spp., being absent from Tortuga Estate and Arena Reserve. *Pheidole* spp. seem to prefer light sandy soils to heavy clay and some 97% of the specimens taken came from River Estate and Arena Reserve. The Ponerine species noted never seem to be present in large colonies, but are fairly evenly distributed over the areas sampled.

It is of interest that, out of the 1260 ants and pupae counted in the litter and 0–3 in. samples, 1117 (88·6%) fell into the five genera estimated separately. Of these 1117 individuals, 910 (81·4%) occurred in the 0–3 in. soil layer, showing that the species were almost certainly true soil-inhabiting forms and not chance migrants on the litter at the time the samples were taken. Another point of interest is the relatively small number of larvae found, indicating either that the colonies are of small size normally, or that the samples were not taken to a depth great enough to penetrate into the nests.

(*b*) *The Acarine fauna*

Check List 3 gives the family and in some cases the generic determinations (made by Dr H. E. Ewing) of the mites taken in the areas sampled. To quote from a letter from Dr C. F. W. Muesebeck: '. . . I am sorry that more definite identifications for the mites are impossible at present. The several large groups of mites that are commonly found in soil and surface litter have been so little studied that specific determinations are altogether impossible in most cases, and even generic placement cannot always be made with safety.'

In all, some 45 species of mites were encountered in these samples. Of these, by far the commonest and most widely distributed were an unknown number of species of Galumnids. Next in frequency came the family Nothridae, especially a species—or complex of species—of the genus *Malaconothrus* and the least common of the estimated species was a series of species probably of the genus *Adoristes*. Members of the family Parasitidae were of wide occurrence, but present in very small numbers in most of the samples taken.

Table 5 gives the quantitative results of the Acarina that were estimated separately.

Of the 6277 mites counted in the litter and 0–3 in. samples, 2942 (46·8%) fell into the five named groups. Of these 2942 individuals 1734 (58·9%) occurred in the surface litter layer, and the rest in the 0–3 in. soil layer.

On the basis of these figures, the Galumnidae form some 30% of the total earth mite population in Trinidad, and the mite population itself some 56% of the total soil arthropod population. A point of some interest shown in Table 5 is the relative abundance of *Adoristes* sp. at Arena Reserve, and Hoplo-

Table 4. *Ant distribution in the areas sampled*

		Tumpuna Reserve				Arena Reserve				Matura Reserve		Brigand Hill Estate				Tortuga Estate				Las Hermanas Estate				River Estate				Totals
		L*	S*	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	S+L
Ponerinae	*Ponera*, 4 spp.	8	—	6	5	—	—	5	2	3	—	—	4	—	—	—	3	—	15	—	—	5	1	1	13	—	5	76
Myrmecinae	*Pheidole*, 5 spp.	1	—	—	—	—	84	2	8	—	—	—	—	—	—	—	5	—	—	—	—	—	—	—	103	—	—	203
	Solenopsis, 4 spp.	—	3	—	—	26	5	9	20	20	14	4	13	—	28	1	11	1	8	—	20	16	2	—	45	29	145	420
Formicinae	*Rhizomyrma*, 4 spp.	—	3	—	74	—	—	—	—	—	5	—	36	1	5	—	—	—	—	—	35	2	59	—	2	—	2	224
	Brachymyrmex, 2 spp.	—	—	—	—	—	—	67	5	—	—	—	26	—	76	—	9	—	9	—	1	—	1	—	—	—	—	194
All genera	Larvae	1	—	2	4	1	—	27	4	7	7	1	3	—	—	—	—	—	1	—	2	—	1	—	11	2	5	83
All other adults and all pupae		5	1	1	4	8	6	4	10	4	3	1	16	1	10	2	3	—	2	—	6	10	23	—	9	6	8	143

Table 5. *Acarine distribution in the areas sampled*

		Galumnidae all spp.	Nothridae *Angelina* sp.	Nothridae *? Adoristes* sp.	Nothridae *Malaconothrus* sp.	Hoplodermatidae all spp.	All other species
Tumpuna Reserve	L*	181	5	—	34	35	327
	S*	60	—	1	16	1	80
Arena Reserve	L	46	6	—	19	15	51
	S	102	—	1	38	10	81
Matura Reserve	L	60	19	14	14	20	146
	S	53	5	18	55	1	71
Brigand Hill Estate	L	98	1	17	31	28	182
	S	101	—	6	28	4	129
Tortuga Estate	L	182	—	7	15	76	210
	S	133	3	5	21	11	143
Las Hermanas Estate	L	36	5	3	10	5	59
	S	28	2	4	15	8	68
River Estate	L	12	6	3	6	8	25
	S	18	2	5	13	3	55
	L	31	4	—	3	6	154
	S	34	2	—	13	2	42
	L	47	2	—	9	4	110
	S	39	—	—	11	5	64
	L	176	11	4	26	37	340
	S	73	2	2	25	7	120
	L	122	4	8	44	16	237
	S	99	—	—	24	6	169
	L	35	15	—	5	10	102
	S	31	—	—	14	2	110
	L	69	6	—	15	8	140
	S	25	1	2	13	5	120
Totals	L+S	1891	101	100	517	333	3335

* L = litter samples; S = 0–3 in. cores of soil.

dermatids at both Arena and Matura Reserves. Jacob (1939) has shown that a subspecies of *Adoristes ovatus* and several species of Hoplodermatids—especially *Hoplophorella thoreaui*—are of considerable importance in the breakdown of spruce and fir needles in forest litter in the United States and, in view of the profusion of living, dying and dead rootlets in the litter and easily penetrable light soils at Arena and Matura, it is tempting to suggest that the abundance of these mites is possibly a result of such profuse root development.

Check List 3. *Mites taken in soil and litter samples*

ORIBATOIDEA	5 sp.
Galumnidae	*Neoribates* sp.
	Galumna spp.
	1 sp., genus unknown
Nothridae	*Angelina* sp.
	?*Adoristes* spp.
	Malaconothus spp.
	Hermaniella sp.
	Subfam. Lohmanninae, 1 sp.
	4 spp., genera indet.
Uropodidae	*Uropoda*, 3 spp.
	4 spp., genera indet.
Hoplodermatidae	2 spp., genera indet.
Hypochthonidae	2 spp., genera indet.
Acaridae	2 spp., genera indet.
Trombidiidae	?1 sp., genus indet.
Erythraeidae	1 sp., genus indet.
Parasitidae	*Atricholaelaps* sp.
	Subfam. Parasitinae—?11 spp., genera indet.

(*c*) *Comparison of the areas sampled*

(1) *Tumpuna and Arena Forest Reserves.* The same plant associations occur under widely divergent soil types. Table 2 shows that the total arthropod populations for litter and soil for both series of samples (litter and 0–9 in., and litter and 0–3 in. for both areas) are probably biologically identical, the difference of some 14% being almost certainly due to the errors of random sampling. But although the two areas show similar numerical populations, the qualitative aspects show that the Tumpuna samples contained representatives of at least ten insect families not encountered at Arena. It would seem that the fauna at Arena is rather more specialized (large numbers of individuals of a few highly adapted species being present) than that at Tumpuna. Amongst the obvious differences shown in the tables and check lists, the occurrence of Nematocerous fly larvae in relatively large numbers at Tumpuna must be noted. Undeniably the soil was much wetter here than at Arena, and therefore in a more suitable state to attract gravid females of moisture-loving flies. Orthoptera were also more numerous at Tumpuna—fourteen newly emerged first instar Acridiid nymphs were found in one litter sample. Termites, although numerically superior at Tumpuna, were probably more prevalent at Arena: 543 workers were counted in one sample at Tumpuna, whereas those taken at Arena were evenly distributed throughout the various samples. The Acarina were identical in both areas. Total Tumpuna population (litter and 0–3 in., litter and 0–9 in.) was 1198 individuals. The total Acarine fauna at Arena (neglecting the 9–15 in. core) was 1183 individuals. Those families and genera that were counted separately, however, show a difference: *Adoristes* sp. is present in far greater numbers at Arena than at Tumpuna, and there is a greater number of Galumnids at Tumpuna, though here the difference is probably not large enough to be significant.

Briefly, then, in this case the crappo-guatecare-cocitore association has produced almost identical numerical but widely differing qualitative populations in two areas on completely divergent soil types.

(2) *Matura Reserve and River Estate.* Widely divergent plant associations occur on comparable silty types of soil. Little reliance can be placed on the comparative results since twice as many samples were taken at River as at Matura, and only the quantitative results for the litter and 0–9 in. samples are strictly comparable. Clearly the numerical populations are of different orders of magnitude—the difference of nearly 38% cannot all be due to experimental error. It is interesting to note that termites are virtually absent from the River plot. The cacao had been clean cleared several years previously, and the cuttings buried in deep pits, and save for a few *Nasutitermes costalis* Holmgr., from carton nests on the trees, no termites were seen. At Matura, however, a species of *Subulitermes* was active on the soil surface beneath the litter, and nests of other unidentified species were noted in rotting wood lying on the forest floor. The Acarina form the main cause of the divergence in population, 914 specimens being taken at Matura as compared with 346 at River. *Adoristes* sp. is present in larger numbers in Matura swamp forest than in the well-drained cacao land at River. Galumnids are again the dominant Acarines, but they occur in far greater numbers at Matura. The Hoplodermatids form another group in which there is a wide divergence—in actual fact the litter samples at Matura gave more than twice as many specimens of this family as any other litter samples taken in the whole investigation. An interesting but puzzling point is that in both areas the dominant ant genus is *Solenopsis*.

(3) *Tumpuna Reserve and Brigand Hill Estate.* Widely divergent plant associations on closely comparable soil types. Tumpuna shows a numerical population more than twice as large as that at Brigand Hill. At least four orders are represented at the former area that were absent from the samples

taken at the latter. The main numerical discrepancy again lies with the Acarina and the Isoptera, although the number of termites at Brigand Hill is greater than at most of the other cacao estates, possibly due to immigrations from a strip of secondary forest bordering one side of the estate. Tumpuna produced four times as many Galumnid mites as Brigand Hill, and also shows an ascendancy in Hoplodermatids, *Malaconothrus* spp. and 'other species'. Possibly the relatively poor Oribatid population at Brigand Hill is partly due to the scant nature of the surface litter. The number of families represented in the areas is almost identical, but several Diptera were found at Brigand Hill and not at Tumpuna, and *vice versa*. The same can be said for beetle families, but too little is known of the habits of either of these groups for any conclusions to be drawn from these facts.

In brief, the arthropod soil and litter fauna of River and Brigand Hill cacao estates is very much smaller than in the pedologically comparable plots at Matura and Tumpuna reserves. This is interesting, and may be an index of regular trampling by the estate labourers cutlassing weeds and harvesting the cacao crop.

(4) *Tortuga Estate, Brigand Hill Estate, and Las Hermanas Estate.* Three cacao estates on soil types with some comparable physical features. It should be noted, however, that the chocolate soil at Tortuga is very exceptional in having an almost perfect combination of those physical and chemical factors conducive to fertility (in an agricultural sense), whereas the clay at Brigand Hill lacks some of the physical factors, and the silty clay at Las Hermanas lacks both physical and chemical factors necessary for this state. A perusal of Table 1 and Check List 1 shows the following points:

The numerical populations of Brigand Hill and Tortuga are biologically identical and less than half that prevailing at Las Hermanas. The discrepancy is largely due to the Acarine population—over 1000 more individuals being obtained at Las Hermanas than on the other two plots. There is also a surprisingly large population of Ortheziine scale insects at Las Hermanas. The writer has found these scales on several occasions with their mouth parts penetrating young cacao rootlets, and it seems as if they may be doing economic damage to the trees when present in large numbers.

Tortuga shows the largest spider population encountered in the whole of the present investigation. It seems possible that these predatory animals might be an important factor in keeping deleterious mites and scale insects under control. It is interesting once more to note the preponderance of Nematocerous fly larvae at Las Hermanas—perhaps an index of the high water table and frequent wet season waterlogging. With regard to the Acarina, Las Hermanas gave far greater numbers of Galumnids, Hoplodermatids and Nothrids of the genus *Malaconothrus* than the other two areas. In view of the similarity of the surface litter in the three areas, it would almost seem that some pedological factor is at work, favouring the optimum conditions for these species at Las Hermanas. These Las Hermanas figures correlate closely with those obtained at Tumpuna, and it is interesting to note that such soil constants as carbon/nitrogen ratio and index of texture are very similar for both areas.

Briefly, although the vegetation on all three estates is identical, the numerical and qualitative aspects of the soil fauna differ—particularly when Las Hermanas is compared with Brigand Hill and Tortuga. Owing to Witches Broom disease and unsatisfactory soil conditions, yields have been very low at Las Hermanas in recent years. The Estate is still tended, however, and weeds are cutlassed and the crop harvested regularly. Trampling is probably not so frequent as at Tortuga or Brigand Hill, and this may certainly be one factor tending towards a high soil population. Again, weak trees may be conducive to the reproduction of scale insects and their attendant ants.

An attempt was made to correlate directly, in the form of graphs, the various soil indices for the seven sampled areas, with the animal population of the 0–3 in. cores. The graphs were, however, singularly disappointing, the points being too few and variously distributed to enable any definite conclusions to be drawn.

5. SUMMARY AND CONCLUSIONS

1. An apparatus for the flotation-extraction of arthropod fauna from soil samples is described, and the sampling and extraction techniques used in the present investigation are shown to be sufficiently accurate for preliminary work on the gross arthropod fauna of soil and surface litter.

2. The ecological environment would seem to have a greater influence on the magnitude of the arthropod soil population than the gross soil type, although the latter undoubtedly has a considerable influence on the type of arthropods inhabiting it.

3. Certain faunal groups (e.g. Hoplodermatid mites, termites, Nematocerous fly larvae) favour more or less specialized habitats, and only occur in large numbers in such habitats.

4. In every locality sampled, the Acarina form the dominant group of soil and litter animals, and their occurrence seems to be related in some cases to the composition and abundance of the surface litter. Although the numerical populations for two or three ecologically different areas may be the same, the qualitative constitution of the populations may differ.

5. Distribution in depth falls off very rapidly

after the first 2 or 3 in. Many forms do not seem to migrate deeper than 6 in. from the soil surface, and only mites and ants appear to occur in any numbers at the 9 in. level. In the light sand sampled at Arena Reserve, however, migration appeared to take place generally down to the 9 in. level, and many mites were found at a depth of 15 in.

6. The occurrence of coccids, and their attendant ants, in relatively large numbers—especially at River and Las Hermanas Estates, both regarded as 'poor' in that the annual yield of cacao has decreased rapidly in the last few years—shows that at least one group of soil insects is probably doing economic damage to a plantation crop in Trinidad, and should provide an incentive for further work on the problem.

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THE ECOLOGY OF CLOSELY RELATED SPECIES WITH SPECIAL REFERENCE TO CORMORANT (*PHALACROCORAX CARBO*) AND SHAG (*P. ARISTOTELIS*)

By DAVID LACK

1. INTRODUCTION

This paper is a sequel to one on the ecological aspects of species formation in passerine birds (Lack, 1944). Gause (1934) contends that two species with similar ecology cannot live in the same area, and in the earlier paper this principle was shown to hold among closely related species of passerine birds, both in Britain and on oceanic islands. Such species either frequent different regions, or different habitats, or, when they live in the same place, they eat mainly different foods, the latter commonly being associated with a difference in body size.

I originally intended to follow this paper with a second one analysing the extent to which the same might apply in British non-passerine birds. Among these birds, examples of closely related species which breed in a similar habitat but in mainly different regions are provided by the mute and whooper swans (*Cygnus olor* and *C. cygnus*), the curlew and whimbrel (*Numenius arquata* and *N. phaeopus*), and the common and arctic terns (*Sterna hirundo* and *S. macrura*). In each of these pairs, the first-mentioned species breeds mainly south of the second. Examples of related species which breed in the same regions but in mainly different habitats include: the long-eared owl *Asio otus* in woods and the short-eared owl *A. flammeus* in open country; the marsh harrier *Circus aeruginosus* in very damp marshland and the Montagu harrier *C. pygargus* in dryer marshland and on heaths; the goosander *Mergus merganser* primarily by swift-flowing streams and the red-breasted merganser *M. serrator* primarily by lochs.

Two species which overlap widely in both region and habitat but differ in food are the hobby *Falco subbuteo* and kestrel *F. tinnunculus*. Both frequent open country with trees in southern England, but the hobby feeds primarily on insects and on small birds caught on the wing, and the kestrel primarily on rodents and to a much smaller extent on small birds and insects caught on the ground. A case of a difference in both habitat and food is provided by the four species of gallinaceous birds in northern Scotland, of which the ptarmigan (*Lagopus mutus*) lives in the alpine zone feeding primarily on *Empetrum* and *Vaccinium*, the red grouse (*Lagopus scoticus*) on moorland feeding primarily on *Calluna*, the black-cock (*Lyrurus tetrix*) on the wood edge feeding primarily on *Betula*, and the capercaillie (*Tetrao urogallus*) in forest feeding primarily on *Pinus* needles. (Though the two latter species are placed in separate genera from the two former, they are probably closely related. In making generic distinctions, undue weight would seem to have been given to male characters. The females of the four species are rather similar in appearance, while interbreeding has been recorded not infrequently.)

In the earlier paper, instances were also given in which two related passerine species frequent the same habitat, but differ markedly in body-size and in food. British non-passerine birds probably provide several further examples, but in most cases insufficient is known of the food of the birds concerned to say whether or not the size difference is correlated with a difference in diet. Examples are the great and lesser spotted woodpeckers (*Dryobates major* and *D. minor*), mallard and teal (*Anas platyrhynchos* and *A. crecca*), great-crested and little grebe (*Podiceps cristatus* and *P. ruficollis*), little, common and sandwich terns (*Sterna albifrons*, *S. hirundo* and *S. sandvicensis*), and several species of gulls (*Larus* spp.).

The idea of a complete survey of British non-passerine birds was eventually abandoned owing to the many cases in which two closely related species appear to overlap widely in ecology, but insufficient is known to state definitely whether or not this is the case. From the information available in general works on British birds, notably Witherby (1938–41), the following species appear to come in this category: tawny and long-eared owls (*Strix aluco* and *Asio otus*), both living in woods and eating similar prey; teal and garganey (*Anas crecca* and *A. querquedula*) on southern marshes and inland waters; gadwall, wigeon and pintail (*Anas strepera*, *A. penelope* and *A. acuta*) on northern waters; and among sea birds, cormorant and shag (*Phalacrocorax carbo* and *P. aristotelis*), storm and fork-tailed petrels (*Hydrobates pelagicus* and *Oceanodroma leucorrhoa*), roseate and common terns (*Sterna dougallii* and *S. hirundo*) and herring and lesser black-backed gulls (*Larus argentatus* and *L. fuscus*).

2. CORMORANT AND SHAG

From the above list, one pair of species has been singled out for detailed analysis. The cormorant and shag are two closely related species, and are suffi-

ciently similar in appearance and habits for inexperienced ornithologists to confuse them in the field. Both are common in Britain and occur round most of the south-west, west and north coasts, but they are absent from most of the east and south-east. Nearly everywhere the shag is much the commoner of the two, but in a few places, such as the Isle of Wight, the cormorant breeds but not the shag. Both species nest on cliffs overlooking the sea, and both feed by swimming under the water for fish. At first sight they appear to overlap widely in ecology, an impression supported by the information in general works on British ornithology. Therefore, since they commonly occur in the same regions, they might be thought to provide an exception to Gause's thesis. Fortunately, sufficient facts are available for a detailed analysis, and this shows that the two species differ widely in both nesting and feeding requirements.

Nesting habitat. Though both species nest on rocky places overlooking the sea, the shag mainly selects caves, holes, hollows among boulders, and narrow cliff ledges. The cormorant, on the other hand, nests chiefly on flat broad cliff ledges and on the flat tops of stacks and islets. Occasionally, as on the Calf of Eday in the Orkneys, the two species nest on the same cliff face; but here the shag nests on the narrow lower ledges and the cormorant on the wide upper ledges and on the flat ground just above the cliff, and there is only an extremely small overlap (Lack, 1943). A similar difference holds for other parts of Europe. For instance, in the Faeroes, Salomonsen (1935) found the shag nesting among boulders at the foot of mountains, and the cormorant on the cliff ledges. On the mainland of Europe, the cormorant also nests inland by fresh waters, sometimes in trees, which the shag does not do.

Food. The information given in general works on British birds and by Collinge (1924–7) suggests that the cormorant and shag eat largely the same types of food. However, Steven (1933) has made a detailed analysis in Cornwall which shows that, here at least, the two species have almost completely different diets, and, moreover, feed mainly in different places. The cormorant feeds chiefly in the shallow waters of estuaries and harbours, also inland on large rivers and on reservoirs. Only occasionally does it forage farther out at sea. On the other hand, the shag feeds mainly out at sea, and seeks food in estuaries and sheltered waters only during stormy weather. Hence the two species rarely feed together.

In Cornwall the staple food of the shag throughout the year is the sand eel *Ammodytes*. Out of 188 birds examined by Steven, just over half contained *Ammodytes*, and 37 % contained nothing else. About one-quarter of the birds contained clupeoid fish, chiefly the sprat *Clupea sprattus*, these fish being taken mainly in winter. On the other hand, only 3 % of the birds had eaten flat-fish, though a special effort was made to obtain shags from estuaries, where they might be likely to feed on them. The number of shags which had eaten shrimps or prawns was also small.

On the other hand, of 27 cormorants examined by Steven, just over half contained flat-fish, 37 % contained prawns and shrimps, while only one had eaten a sprat and none had taken sand eels. The diet was almost totally different from that of the shag, but dragonet (*Callionymus*), wrasse (labrids) and gobies (*Gobius*) were taken in small numbers by both birds. The diet of the cormorant in fresh water was not examined by Steven; the eel *Anguilla anguilla* is known to be a favourite food. The shag does not normally feed in fresh water.

Steven's data show a further difference in the feeding habits of the two species, since the cormorant feeds primarily on fish which live on or close to the bottom, while the shag feeds mainly on free-swimming forms. This suggests that the conclusions given

Table 1. *Differences in diet of shag and cormorant*

Based on 188 shags and 27 cormorants examined by Steven (1933).

A

Food	Percentage of stomachs in which found: Shag	Cormorant
Ammodytes spp. (sand eel)	51	—
Clupea sprattus (sprat)	11	4
Pleuronectids (flat-fish)	3	52
Crangonidae (shrimps)	3	33
Palaemonidae (prawns)	5	15
Ctenolabrus rupestris (gold-sinny wrasse)	13	17
Labrus bergylta (ballan wrasse)	6	15
Callionymus spp. (dragonet)	10	11

B

Food	No. of individuals of each food species, expressed as percentage of all individuals present: Shag	Cormorant
Ammodytes spp. (sand eel)	33	—
Small Clupeoids (sprat, sardine, brit)	49	1
Pleuronectids (flat-fish)	1	26
Palaemonidae (prawns) and Crangonidae (shrimps)	2	33
Labrids (wrasse species)	7	5
Gobius spp. (goby)	4	17
Other kinds	4	17

Note. In Part B, the high total of small clupeoids in the shag stomachs is due to the fact that two individuals between them contained 350 brit. If these had been omitted, the figures for the shag would have been *Ammodytes* 45 %, small clupeoids 31 %.

above apply more widely than to Cornwall alone, though a general survey has not yet been undertaken. It would be of particular interest to make a detailed survey throughout the year in a region where the cormorant comes in contact with different species of *Phalacrocorax* as it does in Australia (Serventy, 1938).

3. OTHER SEA BIRDS

A parallel with the cormorant and shag is provided by two other related species of British sea birds, the common guillemot *Uria aalge* and black guillemot *U. grylle*. The former breeds on cliff ledges and the tops of stacks, the latter in crevices and among boulders. The common guillemot feeds out at sea on free-swimming fish, particularly *Ammodytes*, and in America also on lant and capelin. The black guillemot feeds inshore, primarily on the butterfish (or rock-eel) *Pholis gunnellus*, which lives on the sea bottom, also on molluscs and Crustacea (Bent, 1919; Salomonsen, 1935; Witherby, 1938–41). Hence these two species, like the cormorant and shag, do not seriously overlap in either nesting sites or food. It is interesting that the common guillemot parallels the cormorant in its nesting but the shag in its feeding, while the black guillemot parallels the shag in nesting and the cormorant in feeding.

In the earlier paper it was concluded that the habitat differences between related species are a result of natural selection, each species being better adapted than the other in the habitat where it normally occurs. Consequent on this, each species has evolved behaviour responses enabling it to select its specific habitat. Hence the individuals of two related species rarely come into competition. However, their ecological differences are a result of former mutual competition, and this competitive element is still potentially present. For occasionally an individual breeds outside its specific habitat, and the reason that such cases do not become commoner is presumably that they are quickly eliminated by natural selection.

A parallel argument doubtless applies to the differences in nesting habitat between related species of sea birds, as it is difficult to see how otherwise such differences could persist. But concrete evidence is lacking. Thus it is difficult to see any character which gives the shag an advantage over the cormorant when nesting in caves, boulders, etc., or any which gives the cormorant an advantage on flat ledges. But if an adaptive difference does not exist, the difference in nesting site between the two species is even harder to explain. In the case of the two guillemots discussed above, a probable adaptive difference is known, since it is usually considered that the pointed egg of the common guillemot is less easily rolled over a cliff edge than is the blunter egg of the black guillemot. This does not, of course, account for the avoidance of holes and crevices for nesting by the common guillemot.

Sea birds show all the main types of ecological isolation found in passerine birds—by region, by nesting habitat and by food. In one case there is also isolation by breeding season, since Murphy (1938) states that on Kerguelen Island the tern *Sterna virgata* breeds in October and November, while in January and February the same nesting grounds are used by another species, *S. vittata*. *S. virgata* feeds inland on insects and spiders, *S. vittata* at sea, so the two species also differ in food.

4. ECOLOGICAL ISOLATION IN OTHER ANIMALS

The main types of ecological isolation found in birds are also found in mammals. Thus in Scotland the common hare *Lepus europaeus* occurs on low ground and the mountain hare *L. timidus* on high ground. Barrett-Hamilton & Hinton (1913–14) have provided strong evidence that this habitat difference is due to competition, since Hinton's hare *L. anglicus*, which is a form of the mountain hare, was widespread on low ground in Britain during Pleistocene times, but became extinct after the colonization of the common hare. Further, Ireland appears to have been cut off from England before the arrival of the common hare, and, in the absence of the latter species, the Irish form of the mountain hare is common on low ground. Barrett-Hamilton & Hinton have demonstrated a similar situation in the two European bank voles *Clethrionomys* (*Evotomys*) *glareolus* and *C. nageri*. In western Europe, at the latitude of Britain, the later arrival *C. glareolus* has eliminated the formerly widespread *C. nageri* from the low ground habitats except on a few outlying western islands, such as Jersey, Skomer, Mull and Raasay. Forms of *C. nageri* persist on high ground in western Europe.

In British mammals there are also parallels with those birds in which two related species occur in the same habitat but differ markedly in size, and by inference in food. Huxley (1942) has cited the common and pygmy shrews (*Sorex araneus* and *S. minutus*), and the stoat and weasel (*Mustela erminea* and *M. nivalis*). An example of four mammal species which live in the same habitat but differ in food was cited in the earlier paper for the four Antarctic seals (Lack, 1944). As discussed more fully in the earlier paper, ecological differences are found between species because, in their absence, one species eliminates the other. An example of such elimination is evidently occurring in Britain at the present time, since the native red squirrel *Sciurus vulgaris* is decreasing rapidly before the introduced grey squirrel *S. carolinensis*.

Ecological isolation is also a widespread phenomenon among closely related species of insects. Thus Elton (1927) cites from Shelford (1907) that of the five species of tiger-beetles (*Cicindela*) found round Lake Michigan, each frequents a different habitat. Likewise in many of the phytophagous insects, related species frequent different food plants. However, there are many other insects in which closely related species appear to feed together on the same food plants. In this connexion, G. C. Varley has suggested to me that if the numbers of two related species are controlled primarily by parasites or predators, then they may be greatly below the limit set by food, so that the two species could live in the same area and eat the same types of food without effectively competing. This type of situation is probably commoner in insects than in birds.

Fresh-water biologists have tended to attribute the habitat differences between species to simple behaviour responses towards temperature, salinity, *p*H and other physical factors. But though such responses may account for how each species finds and stays in its habitat, it is also necessary to explain the evolution of the behaviour responses concerned. The latter have presumably been brought about through natural selection, those individuals surviving whose behaviour responses have brought them to a favourable environment, and those being eliminated which found unfavourable environments. I formerly made the same omission in interpreting habitat selection in birds (Lack, 1933, 1944). That the presence or absence of related species is one of the most important factors in limiting the habitats of fresh-water organisms has been clearly demonstrated by Beauchamp & Ullyott (1932) for fresh-water planaria, while another suggestive case is that of the copepod *Eurytemora lacinulata* (Elton, 1927).

It is not the object of this paper to elaborate on ecological isolation in other types of animals or in plants, but merely to draw the attention of specialists in other groups to this problem. Gause's thesis that two species with similar ecology cannot persist together in the same area is logically unassailable when the two species compete for food. Further, it is fully substantiated in wild birds, though superficial appearances often suggest that there is marked ecological overlap—as in cormorant and shag. It would be possible to cite many further cases of ecological isolation in other groups of organisms, but the significant study is to take every species in a whole group, and to analyse how many of them differ from each other in ecology, and in what ways. Particular attention should be given to cases of ecological overlap, as it is extremely difficult to see how these could occur except (*a*) temporarily, where one species is in process of eliminating another, (*b*) in an area where two species meet along an environmental gradient, one end of which favours one species and the other end the other, and (*c*) where the species do not compete for food, but are kept in check by predators or parasites.

There is the further important problem of how ecological differences arise. Huxley (1942, pp. 265–84), who cites numerous further cases of ecological isolation in both animals and plants, suggests that ecological differences have led to the origin of new species. In birds, on the other hand, I consider that new species have arisen primarily through geographical isolation, and that ecological isolation is enforced through competition when two species later meet in the same area. The arguments for this are set out in the earlier paper, and in more detail in a book (Lack, 1944, and *in press*). The extent to which these views may hold in other animals and in plants is a subject for future research.

5. SUMMARY

1. Many closely related species of British non-passerine birds differ in their ecology, but in other cases there is apparently an overlap.

2. In one case of apparent overlap, that of the cormorant *Phalacrocorax carbo* and shag *P. aristotelis*, close analysis shows that in fact the two species differ markedly in both nesting sites and food.

3. Ecological separation may be through a difference in region, habitat or food, while in one case in terns there is isolation by breeding season.

4. The main types of ecological isolation found in birds are also found in mammals, and the subject should be further investigated both in other groups of animals and in plants.

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OBSERVATIONS ON CLIMATE AND SEASONAL DISTRIBUTION OF MOSQUITOES IN EASTERN COLOMBIA*

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(With Plate 1 and 3 Figures in the Text)

1. INTRODUCTION

There is a considerable literature on variation in seasonal abundance of mosquitoes, particularly of anophelines, because of the importance of this subject in relation to malaria studies. Of much interest also, from the point of view of general biology, are studies of seasonal fluctuations in mosquito populations. Students of the statistical aspects of natural selection and of the distribution of genetic factors in populations have pointed out that the spread of variants through a population is bound to depend in great part on the nature of the fluctuations in population density, and the subject of seasonal and annual cycles has thus become of basic interest in relation to the processes of evolution. Such studies also form an integral part of any ecological work, since the environmental characteristics change in time as well as in space, and the adaptations of a particular species to factors in the physical environment may be as clearly shown by the seasonal distribution of the species as by its habitat distribution. A recent study at Villavicencio, Colombia, though fragmentary in itself, may have particular interest in these connexions because this locality is in the forested section of interior South America—a region of surpassing biological interest, on which there is almost no quantitative information available.

The work at Villavicencio is oriented primarily toward the study of the epidemiology of jungle yellow fever, hence attention has centered on the mosquito *Haemagogus capricornii*, which field work indicates to be the chief vector of the virus of yellow fever in the region (Bugher, Manrique, Garcia & Mesa, 1944). Attempt has been made, however, to keep the collection of data on a sufficiently broad basis to serve as part of a general study of the environmental relations of the mosquito fauna of this sample area of the American tropics, and the present article is written from the latter point of view. Some general notes on the methods of work were included in a previous article on the stratification of diurnal mosquitoes in the forest habitat (Bates, 1944*a*).

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2. CLIMATE

Routine climatic measurements made at the laboratory at Villavicencio are summarized in Tables 1–4. For our purposes it is most satisfactory to break the year at the first of March instead of the first of January. March is the zero month both for yellow fever and for the mosquito vectors; the events of January and February are essentially the closing phases of the preceding annual cycle, and the new cycle of rain, mosquitoes and yellow fever starts toward the end of March.

Perhaps the most striking characteristic of the Villavicencio climate is its uniformity through the year. There is a fairly regular annual cycle from the warm and dry months of January, February and March to the cold and wet months of May, June and July, but the annual oscillations occur within quite narrow limits. The maximum difference is in rainfall, and the least difference is in temperature. There is, however, a clear annual cycle in most biological phenomena which seems to be correlated with the rainfall. During the three years of observation the driest month has been February, and the months of December to March constitute a fairly well-defined dry season. The total amount of rain in these months may seem large, but the high evaporation rate and rapid run-off mean that this rainfall is below what might be called the 'threshold of effective precipitation'. Some streams and ground pools become continuously or intermittently dry, a few species of forest trees shed their leaves, the water table falls markedly, and so forth. This dry season is followed immediately by the period of heaviest rainfall (April and May), and these two conditions together seem to control the annual fluctuations in mosquito populations. Climatic differences in the period between June and November seem to be slight and irregular.

Villavicencio is situated 4 degrees north of the equator, at the base of the Eastern Andes. The streams here form part of the Orinoco system; but the drainage 200 km. south is Amazonian, and the foothill forests of the two drainages are continuous. The Eastern Andes rise very abruptly from the great plains of eastern Colombia, and the high precipitation measured at Villavicencio (4–5 m.) is dependent on this fact. The rainfall about 15 km. east of Villavicencio, away from the mountains, is only half as great (2·5 m. in 1943), though with a similar seasonal

distribution.* Data, in part fragmentary, from various parts of the forested regions of the upper Orinoco and Amazonian drainages seem to indicate that the annual precipitation over most of this area is about 2·5–3·0 m. Temperature conditions over much of the area seem to be closely similar to those recorded at Villavicencio.

and Cauca valleys, where there are two annual rainy seasons and two dry seasons. In the lower portions of these valleys a heavy forest is supported by a precipitation that seems to be generally between 2 and 3 m. annually. It may be noted that the Villavicencio area has the highest rainfall of any part of Colombia for which records have been seen, with

Table 1. *Rainfall at laboratory station, Villavicencio*

	1941		1942		1943		Mean	
Month	mm.	days	mm.	days	mm.	days	mm.	days
Mar.	211·0	14	304·0	18	116·0	12	210	15
Apr.	435·0	22	502·5	20	603·5	26	514	23
May	659·5	24	775·0	27	634·5	23	690	25
June	334·5	28	417·5	21	625·5	29	459	26
July	346·0	30	534·0	25	403·5	27	428	27
Aug.	502·0	27	508·0	21	618·5	24	543	24
Sept.	488·0	22	468·5	16	617·0	18	524	19
Oct.	505·0	27	395·0	21	594·5	24	498	24
Nov.	155·5	16	500·5	20	247·0	16	301	17
Dec.	136·0	12	313·0	18	296·0	13	248	15
Jan.	161·0	10	161·0	19	108·0	6	143	12
Feb.	30·5	7	108·5	13	123·5	7	87	9
Totals	3964·0	239	4987·5	239	4987·0	225	4645	236

Table 2. *Mean temperatures at laboratory station, Villavicencio* (°C.)

Month	1941	1942	1943	Mean
Mar.	28·2	27·8	26·5	27·5
Apr.	27·2	27·2	26·0	26·8
May	26·7	25·8	26·0	26·1
June	25·1	25·2	25·4	25·2
July	25·8	24·7	24·5	25·0
Aug.	26·4	26·3	25·7	26·1
Sept.	27·0	26·7	26·7	26·8
Oct.	27·1	26·7	26·8	26·8
Nov.	27·1	26·9	27·1	27·0
Dec.	27·0	25·9	26·9	26·6
Jan.	27·9	26·5	26·9	27·1
Feb.	28·2	26·8	28·4	27·8
Mean	27·0	26·4	26·4	26·6

Table 3. *Mean percentage relative humidity at noon in shade at laboratory station, Villavicencio (taken with sling psychrometer)*

Month	1941	1942	1943	Mean
Mar.	64·4	68·2	67·4	66·6
Apr.	71·3	61·9	73·4	68·9
May	77·0	76·2	72·7	75·3
June	76·6	75·9	74·6	75·7
July	70·9	73·5	78·3	74·2
Aug.	78·0	70·0	75·9	74·6
Sept.	70·2	70·2	72·4	70·9
Oct.	74·2	69·7	71·9	71·9
Nov.	71·0	70·1	72·5	71·2
Dec.	66·5	69·6	70·5	68·9
Jan.	62·6	66·3	65·3	64·7
Feb.	62·7	64·6	62·7	63·3

Table 4. *Total monthly evaporation in mm. from free water surface protected against sun and rain, laboratory station, Villavicencio*

Month ...	Mar.	Apr.	May	June	July	Aug.
1942	162	108	63	64	68	98
1943	130	68	64	58	54	72
Month ...	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
1942	100	92	90	94	100	108
1943	91	87	108	114	141	146

Some data on 'Colombian climatology' have been summarized by Chapman (1917, pp. 79–83). He describes the conditions that prevail in the Magdalena

* We are indebted to the Meteorological Department of the Aerovias Nacionales de Colombia for these data and for rainfall records from their airports in various parts of Colombia.

the exception of the Pacific coastal strip (Buenaventura), which has about 7 m. annually.

3. METHODS OF MOSQUITO CAPTURE

Two methods of checking on the abundance of mosquitoes have been used in gathering the material on which the present study is based: for diurnal mos-

Photo 1. Capture stations in the Forzosa Area ('B–0' and 'B–6') with arrangements for making simultaneous captures at different levels. Although the platform in this tree is only 6 m. above ground level, the mosquito fauna sampled in the two stations is significantly different.

Photo 2. 'Egyptian type' of stable trap used for sampling the nocturnal mosquito fauna; a donkey is used as bait.

quitoes, the number coming to bite a man in an hour; for nocturnal species, the number caught per night in a stable trap baited with a donkey. The method of arriving at a man-hour rate has been described in some detail in a previous article (Bates, 1944*a*). For the purpose of checking on seasonal shifts in the fauna, man-hour rates are used from the following forest stations: Forzosa Area (foothill forest), two ground stations and the corresponding tree stations, collections being made twice weekly; Cuchilla Area (transition between foothill and piedmont forest), three ground and three tree stations, with collections once weekly; Ocoa Area (piedmont forest), two ground and two tree stations, with collections once weekly. The rate for a given week is thus the mean of 18 man-hours of capture in a selected series of forest environments; by balancing tree and ground stations, an effort is made to eliminate the possible effect of shifts in stratification on seasonal records. Pl. 1, photo 1 shows one of these forest capture stations (Forzosa, tree B).

The stable trap data are taken from captures made in an 'Egyptian type' trap (Pl. 1, photo 2) which has been kept continuously in a roadside clearing near the Ocoa forest for three years. Captures are made three times a week, using donkeys as bait. Notes on the construction and use of this type of trap have been given in a recent article (Bates, 1944*b*).

4. SEASONAL INCIDENCE OF *HAEMAGOGUS CAPRICORNII*

Since most attention was given to the presumed yellow fever vector, *Haemagogus capricornii*, it may be well to consider the behaviour of this species first and in some detail. This mosquito is common in all types of forest in the Villavicencio area, and the larvae have been found in various arboreal container habitats, particularly tree holes. The eggs are able to resist desiccation for long periods of time, thus providing a mechanism for carrying the population through periods of drought. Larval development is moderately rapid. Under laboratory conditions the mean larval life in one experiment was 11·1 days at 30°C., with some larvae completing development in 7 days. This is a higher temperature than would be encountered in nature; and it is in any event hazardous to generalize from growth experiments under laboratory conditions without checks in natural breeding places. It seems likely, however, that development normally requires 2–3 weeks and that the minimum time requirements for a generation would be on the order of magnitude of a month. It is probable that the adults are relatively long lived under forest conditions, though there is no direct evidence on this point. They are very difficult to maintain under normal laboratory conditions, but with special techniques it has been possible to keep significant numbers of adults alive in the laboratory for periods of over 30 days at moderate temperatures (25 and 27°C.); it would seem necessary to postulate a relatively long adult life in nature in order to account for virus transmission.

The diagram for the *Haemagogus* population shown in Fig. 2 seems to be typical for the Villavicencio area: the populations in all three forests studied showed very similar distributions both in 1942 and 1943. The adult population is maintained at a low level during January, February and March, increases rapidly through April and May to reach a peak in June, then declines through July and August to a moderate level, which is maintained through December. The controlling factor in adult abundance thus seems to be the January–March dry season and the following heavy rains.

Weekly data on dry season conditions in relation to *Haemagogus* abundance in the Forzosa study area during 1943 are charted in Fig. 1. 'Level of water in test containers' represents the mean depth of water in six tin cans attached to the trunk of a tree: two 1 m. above ground, two at 14 m., and two at 24 m.

Table 5. *Contrast between maximum and minimum monthly catches of* Haemagogus capricornii *in the three forest areas during* 1943

(Mosquitoes per man-hour.)

Area	Maximum catch	Minimum catch	Proportion max./min.	Month of Max.	Month of Min.
Ocoa	5·9	0·2	29	May	Feb.
Forzosa	19·4	0·1	194	June	Feb.
Cuchilla	17·8	1·1	16	June	Mar.
General mean	15·5	0·6	26	June	Mar.

Checks were also kept on the amount of water present in ten tree holes, and fluctuations in the tree holes were found to be roughly comparable with those recorded in the tin cans, though more variable because of the differences in rate of water loss through seepage, etc. The tin cans seem to be a good index of the relation between water loss through evaporation and water gain through rainfall in forest container habitats. It seems clear that *Haemagogus* abundance is related to water available in the breeding places and that the rainy season increase in adult population is due to the hatching of eggs placed at a relatively high level in the breeding places.

One of the basic questions of yellow fever epidemiology is: can the virus be maintained through the dry season in the mosquito? If mosquitoes become too rare during the dry season to maintain the normal mosquito-mammal cycles, some virus 'reservoir' must be postulated and searched for. Table 5 was prepared with this question in mind. The data in Tables 8 and 9 show the general trend of fluctuations in the populations of *Haemagogus capricornii* (charted in Fig. 1); and this trend seems to be similar in each

of the three forests on which the data are based. But, as is shown in Table 5, there are very significant differences between the forests. The population is relatively small in the Ocoa area; Forzosa and Cuchilla show generally similar densities, but in the dry season adult mosquitoes become much rarer in Forzosa than in Cuchilla. Absolute contrasts in abundance would probably be greater than shown by these monthly means, but the means are probably a better index than absolute maximum and minimum captures would be, since individual captures may reflect meteorological or other transient conditions.

5. SEASONAL INCIDENCE OF OTHER MOSQUITOES

The data on the more abundant mosquitoes of the region have been summarized in Tables 6–9, and the figures for 1943 have been charted in Figs. 2 and 3.

(*a*) *Mosquitoes that breed in permanent or semipermanent pools*

Anopheles rangeli. This is the common 'tarsimaculatus' anopheline of the Villavicencio area. The adults are difficult to distinguish from some of the other species of the group; but the eggs are very distinct,

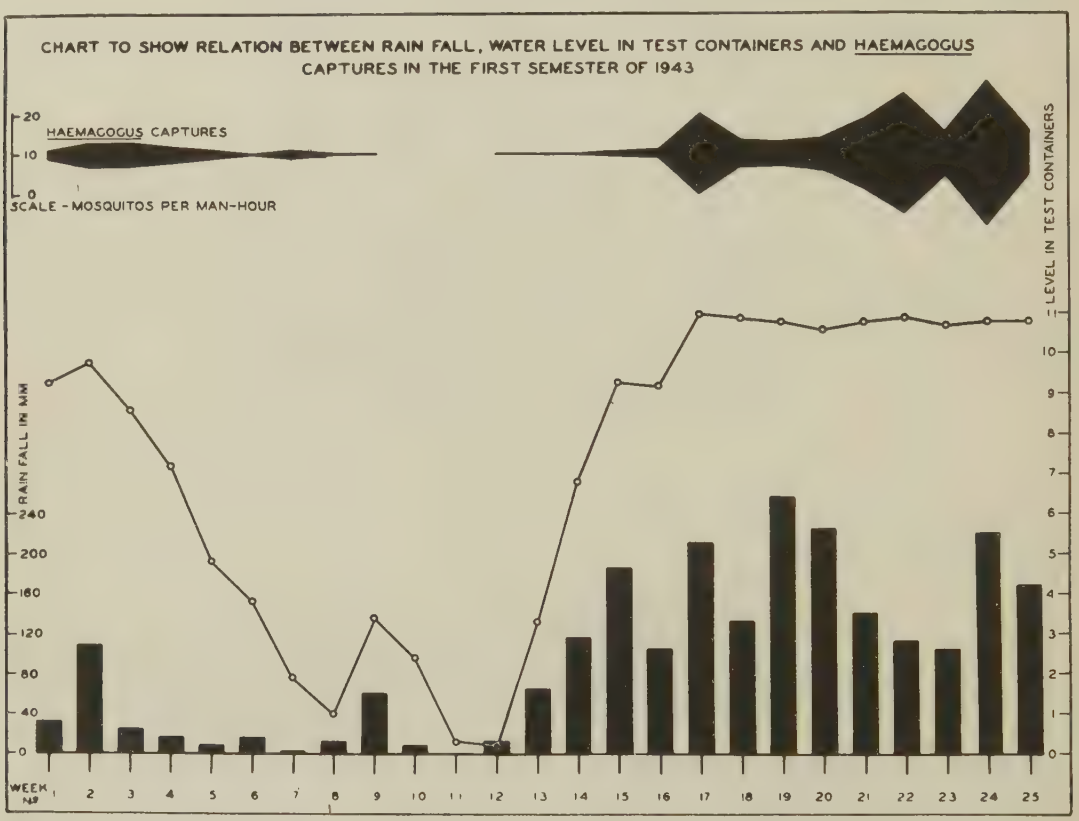

Fig. 1.

From this table it would seem rather unlikely that a series of virus cycles could be maintained throughout the year under Forzosa conditions (variation of 1:194 in density of *Haemagogus*), but perfectly possible that it should be maintained under Cuchilla conditions (variation 1:16). These two areas are only about 2 km. apart, but they may indicate, in miniature, differences between the larger geographical areas in which yellow fever is endemic and in which it is epidemic. Forzosa is on the brow of a hill, Cuchilla in a ravine; and one's first thought is that the ravine conditions may result in greater dry season humidity, permitting greater continuity of breeding places.

and series of females have been kept at different times of year for oviposition so that the species could be determined exactly. Adult identifications, with this check, have always been over 90% correct, so that our figures are sufficiently reliable for the study of seasonal trends of this species. It is notable that the species was about ten times as abundant in the 1942 captures as in those of 1943; this probably represents extreme conditions, as the partial data available for 1941 and 1944 indicate intermediate populations. Such differences might also, however, reflect the technical limitations of the trapping method: inevitable changes in vegetation in the vicinity of the trap

Table 6. *Captures in the Ocoa stable trap*, 1942*

Month	No. trials	*Anopheles rangeli*	*Culex* spp.	*Mansonia* sp.	*Psorophora cingulata*	*Psorophora ferox*	*Aedes serratus*	Total
Mar.	14	122	3·4	5·4	2·5	0	0·1	135
Apr.	13	192	9·2	26	50	0·1	9·2	284
May	12	553	19	18	142	2·0	21	766
June	14	326	37	47	82	0·6	28	528
July	13	260	50	42	89	0·6	29	484
Aug.	13	98	26	55	126	0·8	42	351
Sept.	13	25	16	37	28	0·2	9·1	118
Oct.	12	26	12	46	23	0	1·3	110
Nov.	13	26	24	52	14	0·3	2·6	122
Dec.	13	49	40	25	7·3	0·3	2·2	125
Jan.	12	58	32	17	5·7	0·2	1·2	127
Feb.	12	32	15	4·3	1·4	0·1	0·8	54
Total no. specimens		22,750	3662	4824	7333	67	1930	41,244

* Mean number of mosquitoes per trap night; 'totals' include all mosquitoes caught and are thus larger than the sum of the species specifically identified. Means are given as whole numbers except where the mean is less than 10, in which case the result is carried to the first decimal place.

Table 7. *Captures in the Ocoa stable trap*, 1943*

Month	No. trials	*Anopheles rangeli*	*Culex* spp.	*Mansonia* sp.	*Psorophora cingulata*	*Psorophora ferox*	*Aedes serratus*	Total
Mar.	9	30	3·3	5·7	1·4	0	0	37
Apr.	12	29	12	2·0	7·7	5·0	0·9	52
May	13	45	24	37	89	3·0	6·7	210
June	14	47	46	58	58	2·7	3·9	219
July	15	21	30	11	28	0·6	1·5	91
Aug.	13	13	30	10	9·1	0·1	0·5	66
Sept.	15	7·1	27	5·2	16	0·1	0·6	56
Oct.	12	9·6	26	13	15	0·1	0·8	65
Nov.	13	3·8	28	2·7	32	0	0·7	69
Dec.	14	6·4	29	4·0	15	0·1	2·4	56
Jan.	12	8·7	23	3·0	12	0·2	1·1	49
Feb.	13	12	13	1·3	3·4	0·1	0·2	32
Total no. specimens		2993	3866	2047	3851	102	258	13,319

* See footnote to Table 6.

Table 8. *Standard captures of diurnal forest mosquitoes*, 1942

(Mosquitoes per man-hour.)

Month	*Haemagogus capricornii*	*Psorophora ferox**	*Aedes serratus**	*Aedes dominici*†	*Aedes leucocelaenus*†	*Anopheles boliviensis*†	*Sabethes cyaneus*	*Sabethes belisarioi*	*Sabethoides imperfectus*
Forzosa only:									
Mar.‡	3·0	—	—	0	0	0	—	—	—
Apr.	6·9	—	—	0·2	0·1	0	—	—	—
May	19·1	—	—	0·3	0·5	0·2	—	—	—
June	39·0	—	—	0·6	0·7	0·3	—	—	—
July	17·5	—	—	0·9	0·8	1·3	—	—	—
Aug.	13·0	—	—	0·6	0·5	1·2	—	—	—
All stations: comparable with 1943:									
Sept.	7·9	4·8	2·8	0·5	0·2	0·8	1·0	0·3	0·8
Oct.	5·6	1·3	1·5	0·3	0·2	1·0	0·2	0·5	1·0
Nov.	7·6	4·2	4·4	0·3	0·3	0·7	0·2	0·8	1·0
Dec.	4·5	2·3	7·7	0·3	0·1	0·4	0·03	0·8	0·5
Jan.	3·8	2·6	7·6	0·2	0·1	0·1	0·1	0·9	0·3
Feb.	1·0	0·9	2·1	0·1	0·1	0·1	0·2	0·4	0·5
Total no. specimens	6847	252	445	234	191	353	153	304	349

* Based on Ocoa captures only. † Based on Forsoza and Cuchilla captures only.

‡ 2 hours of capture only in March 1942.

Table 9. *Standard captures of diurnal forest mosquitoes*, 1943

(Mosquitoes per man-hour.)

Month	*Haemagogus capricornii*	*Psorophora ferox**	*Aedes serratus**	*Aedes dominici*†	*Anopheles boliviensis*†	*Sabethes cyaneus*	*Sabethes belisarioi*	*Sabethoides imperfectus*
Mar.	0·6	0	0·4	0·1	0·1	0·2	0·3	0·6
Apr.	5·9	2·2	5·4	0·3	0·6	0·2	0·2	0·4
May	11·5	9·7	8·3	0·5	0·8	0·2	0·2	0·7
June	15·5	10·3	9·5	0·3	1·9	0·3	0·4	0·9
July	9·4	3·7	2·0	0·2	0·8	0·3	0·2	1·1
Aug.	9·2	0·9	3·3	0·3	1·0	0·4	0·2	0·8
Sept.	3·7	1·0	2·5	0·2	0·6	0·4	0·2	0·8
Oct.	4·5	2·9	2·4	0·1	0·4	0·3	0·2	1·1
Nov.	4·9	1·6	6·5	0·1	0·3	0·1	0·3	0·9
Dec.	3·9	3·0	10·3	0·1	0·2	0·1	0·4	0·8
Jan.	0·8	1·3	4·7	0	0·1	0·1	0·2	0·8
Feb.	0·7	0·1	0·6	0	0	0·1	0·1	0·4
Total no. specimens	5578	651	993	129	410	217	227	749

* Based on Ocoa captures only. † Based on Forzosa and Cuchilla captures only.

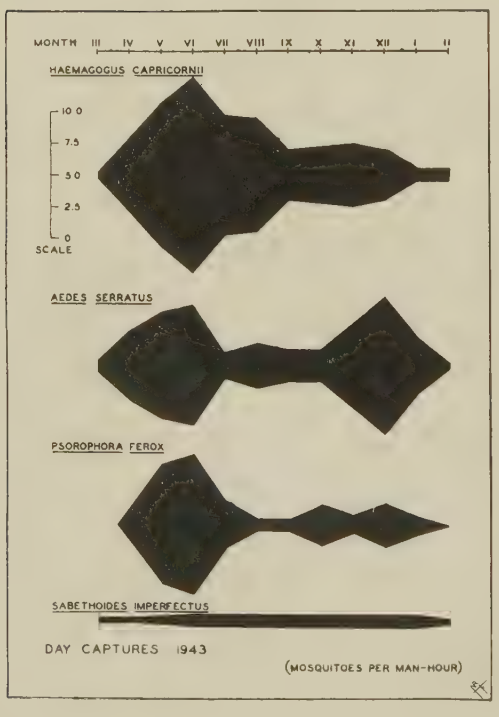

Fig. 2.

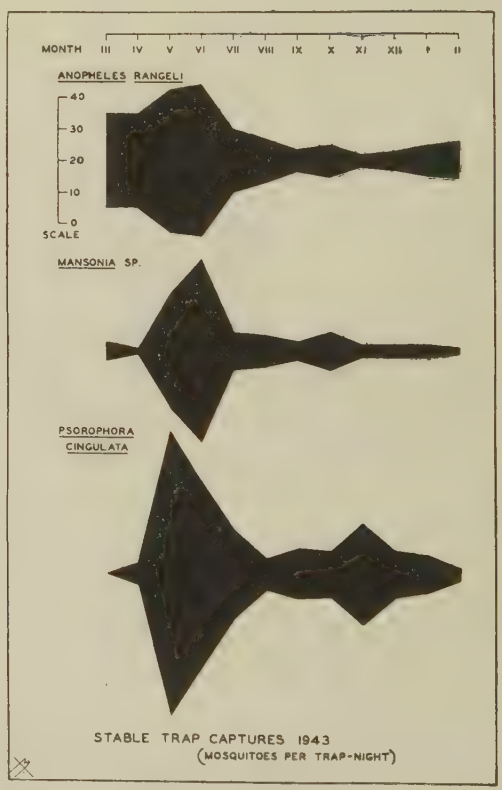

Fig. 3.

(standardization is difficult with tropical growth), differences between donkeys used as bait during the two years, or even slight changes in the trap in the course of wear and repair. The trend of the curves during the two years, aside from this difference in magnitude, is very similar, the population rising to a peak in May and June and falling off during the rest of the year.

Anophelines, like *rangeli*, have no known mechanism for aestivating, or passing an unfavourable season, so that variations in the adult population represent actual fluctuations in the total species population. With *Haemagogus capricornii* and similar mosquitoes a rise in adult population may represent merely the hatching of eggs that have lain dormant. The known breeding places of *rangeli* (sunny ponds, roadside ditches) increase in number and extent with the onset of the rains in April; but from May to December they show very little fluctuation, so that the decrease in population is probably not reflecting any contraction of the area available for breeding. Since the physical environment remains quite constant during this period, the decrease would seem to represent some change in biological relationships (e.g. prey-predator balance). The method of making periodic checks on the relative abundance of all larval stages as well as adults, used in studies of *Anopheles maculipennis* in Albania (Bates, 1941), might give valuable results in studying such a situation.

Mansonia sp. The *Mansonias* caught in the trap seem always to be one species (*fasciolata*), but no careful check has been kept. The trend is similar to that shown by *Anopheles rangeli*; the maximum population level seems to have been similar in 1942 and 1943, but the population was maintained at a high level longer in 1942.

Culex spp. This is a miscellany of many species lumped together, and there is no way of determining whether any particular species would show characteristic seasonal changes. The only interest in the figures is that they show *Culex* species always to be fairly numerous in the trap catches. Most of these species would be pond breeders; a few would be container breeders. But none, so far as we know, has a mechanism for aestivation.

(*b*) *Mosquitoes that breed in temporary pools*

Aedes serratus, *Psorophora ferox* and *P. cingulata* belong to this group. The capture data are from the Ocoa study area only, since these species are common only in level forest where they breed in the transient forest floor pools. All of them may show very abrupt variations in abundance, depending on the degree of inundation of these pools, variations that are somewhat masked by the monthly means that are used in the tables. During the dry season they may disappear completely for weeks at a time, though a very heavy mid-dry season rain will always be followed by the appearance of a few of these mosquitoes about a week later. *Aedes serratus* and *Psorophora ferox*, both diurnal species and usually found breeding in the same pools, as a rule show parallel fluctuations in abundance. It is curious that the December peak of *serratus* in 1943 (Fig. 2) has no *ferox* counterpart. Both species are occasionally caught in the stable trap (probably during the late afternoon and early morning hours), and it is interesting that the stable trap catch of *serratus* in 1943 showed the same bimodal distribution (Table 7) as the day captures (Table 9). This serves as a rough check on the two methods of sampling. The two types of capture were made in the same forest, but in very different situations and perhaps half a kilometer apart.

(*c*) *Mosquitoes that breed in natural containers*

The term 'natural container' was introduced by Shannon (1931) to cover a great class of breeding places of tropical forest mosquitoes: tree holes, water-containing plants, water in fallen leaves, flower parts and fruits. Shannon's classification of these habitats has been adopted and expanded by Hopkins (1936) in his study of African mosquito larvae. Container habitats are all very 'specialized', requiring peculiar modifications of behaviour and physiology on the part of the inhabitants, and a particular species of mosquito is usually sharply restricted to a particular kind of container habitat. The majority of the diurnal forest mosquitoes of South America breed in such habitats, and in mountain forests these are the only habitats available except the limited situations associated with mountain streams. Where container habitats show a seasonal cycle of availability, some mechanism for the carry-over of the mosquito population would seem necessary, and most species (particularly the sabethines and aedines) have eggs that are able to resist long periods of desiccation. The complications of life in a container habitat are well shown by the life history of the only Nearctic sabethine, *Wyeomyia smithii*, which lives in pitcher plants (*Sarracenia*) (Howard, Dyar & Knab, 1915, pp. 94–101).

Aedes dominici. This is perhaps a mixed category, as some of the related species can only be distinguished by the male genitalia (for comment on these identifications, see Bates, 1944*a*). The larvae live in water in bromeliads, which are not common in the particular forests where our studies were made, so the data are hardly extensive enough to be significant. It is notable that a few specimens were caught in all months except March 1942 and January and February 1943, and that there was a slight peak in July 1942 and May 1943.

Aedes leucocelaenus. Only 82 specimens were caught in 1943, and these show no clear distribution pattern, a few being caught every month in the year, with an apparent peak (17 specimens in 60 hours) in September; the apparent peak in 1942 (Table 8) was earlier. This species has very similar habits, both as

larva and adult, to *Haemagogus capricornii*, and its apparent failure to show correspondingly great differences in seasonal incidence is curious.

Anopheles boliviensis. This species, like *Aedes dominici*, breeds in bromeliads. The capture data must be viewed with some suspicion because the species has predominantly late diurnal and crepuscular habits, and the captures were made at midday. The captures would seem to indicate a fairly uniform distribution between April and October, with a slight peak in June.

Sabethes cyaneus, *S. belisarioi*, *Sabethoides imperfectus*. The uniform level of capture of these three species through the year is striking and surely significant. *Imperfectus* is the most abundant, and its continued appearance in dry-season catches is very notable; in January and February it may outnumber *Haemagogus capricornii* in the captures. The chart (Fig. 2) shows this uniform distribution of the adult population. *Sabethes belisarioi* seems at times to show a definite increase under dry season conditions. All three species presumably breed in arboreal containers, though our knowledge of their larval habitats is inadequate. We have found that the eggs of *Sabethoides imperfectus* can withstand desiccation under laboratory conditions.

6. DISCUSSION

Mosquito life histories fall into two broad classes: the one in which development and reproduction is a continuous and regular process, and the other in which development may be interrupted at some stage of growth. The latter type of life history is illustrated by the various hibernation mechanisms of temperate zone mosquitoes, perhaps best summarized in Marshall's book (1938) on the British mosquitoes. Three types of hibernation mechanism are known, depending on whether the egg, larva or adult is involved. It is possible that corresponding mechanisms for aestivation exist in tropical mosquitoes, though the only well-known type of developmental interruption involves the egg stage. Most aedine mosquitoes (a broad grouping, including *Aedes*, *Haemagogus* and *Psorophora* in our fauna) have eggs which may lie dormant for long periods of time, hatching only after receiving an appropriate stimulus. This phenomenon seems to be similar in the temperate and tropical species of the group, though the precise type of stimulus necessary for hatching seems to be characteristic of the species, or perhaps even of the strain, of mosquito. There is an extensive literature on egg-hatching stimuli, and the results obtained by various workers are in part contradictory, perhaps because of failure to realize that a stimulus effective for one species may not be adequate for another. The mechanism in *Aedes aegypti* has been studied at length by Buxton & Hopkins (1927) and Shannon & Putnam (1934) and in certain North American *Aedes* by Gjullin, Hegarty & Bollen (1941). It seems very likely that the sabethine mosquitoes (e.g. *Sabethes*, *Sabethoides*, *Wyeomyia*) may show a similar phenomenon; but this has been described for only a few species. There is some difference of opinion as to whether embryonic development is ever suspended in the anopheline mosquitoes, though it seems clear that no such mechanism is present in the great majority of species.

This factor of possible suspension of development at some stage of growth must be taken into account in evaluating the significance of fluctuations in populations of adult mosquitoes. In *Anopheles rangeli* and similar mosquitoes, for instance, development seems to be purely a function of time and temperature; in a uniform climate such as that of Villavicencio the fluctuations of adult population would then be an accurate index of fluctuations in the total species population. In the case of a mosquito like *Haemagogus capricornii* or *Aedes serratus*, however, a large and unknown fraction of the total species population may be lying dormant at any one time. The species is thus buffered against temporary adversity, and the extent of seasonal and annual fluctuation in the total population would be very difficult to calculate.

Anopheles rangeli, in both 1942 and 1943, was about ten times as abundant at its population peak as at its population minimum, and on the average it was about ten times as abundant in 1942 as in 1943. It would thus seem that a mosquito population, in the relatively constant environment of Villavicencio, can show a population fluctuation over a two-year period of the order of magnitude of 1:100. It may be that these two years represent extreme conditions, since the partial records available for 1941 and 1944 indicate an intermediate population level. An even greater order of magnitude of population fluctuation is indicated by the data obtained by Kumm & Zúniga (1944) for *Anopheles albimanus* and *A. pseudopunctipennis* in El Salvador, where climatic cycles are more marked than in Villavicencio.

The suspension of embryonic development for indefinite and varying lengths of time, shown by aedine and probably by sabethine mosquitoes, very likely results in a more stable total species population, though this is perhaps not so in species that hatch freely on the application of a comparatively slight stimulus to the eggs (e.g. *Psorophora cingulata*, the eggs of which hatch at once on immersion in plain rain water). An investigation of this subject, taking into account the oviposition habits of the adult, the type of stimulus required for egg hatching and the speed of larval development, would undoubtedly yield results of considerable interest. From the point of view of yellow fever epidemiology, however, the fluctuations of the adult population alone must be taken into account, since there is no evidence that the virus can pass from an infected mosquito to the next generation.

7. SUMMARY

1. Weekly captures of diurnal mosquitoes were made in three study areas of Villavicencio, in the forest region of Colombia, over a two-year period; and data on the abundance of nine of the more common types are given. Captures of nocturnal mosquitoes with a stable trap were made in one area at the same time, and data on six mosquito types from these captures are given.

2. Most species show well-marked trends in adult abundance, the peak for most types being in May and June, immediately following the dry season. A few species of diurnal forest mosquitoes, however, show a remarkably uniform level of abundance throughout the year.

3. It is pointed out that adult mosquito abundance has a quite different meaning, depending on whether the development of the mosquito is continuous or interrupted at some stage of growth. The ability of the eggs of aedine mosquitoes to lie dormant for long periods of time provides a buffer against adverse conditions, and modifies the significance of the adult population present at any given period.

4. Data are given on rainfall, temperature, noon humidity and evaporation over a three-year period at Villavicencio. The climate in this area is remarkably uniform. There is an annual dry season, well marked but not severe, usually extending from December through part of March, which seems to be the controlling factor in seasonal fluctuations in biological phenomena.

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THE AGE AND GROWTH OF EELS (*ANGUILLA ANGUILLA*) FROM THE WINDERMERE CATCHMENT AREA

PART I

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(With Plate 2 and 6 Figures in the Text)

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1. INTRODUCTION

The fresh-water eel, *Anguilla anguilla* (L.), has been a food fish in this country for many centuries, and its capture formed one of the earliest inland-water fishing industries. Enormous numbers of elvers enter the rivers of the British Isles and give rise to a considerable population of yellow and silver eels. In spite of this abundance and the good marketable value of eels the fishery for eels in this country has declined and many tons have been imported annually from the Continent to supply the home market. This importation stopped when the war began in 1939, and the Ministry of Agriculture and Fisheries encouraged the capture of both yellow and silver eels in British fresh waters. Contemporaneously with the Ministry's practical efforts, research on the natural history of the eel, particularly yellow and silver eels, while in fresh water has been carried out at the Freshwater Biological Association's laboratory at Wray Castle, where, also, experimental work is being done on methods of catching eels.

On the Continent the eel in fresh water, that is the elver, the yellow and the silver eel, has been the subject of much research, that on the yellow and silver eels dealing chiefly with the age, growth and habits of the fish. Growth studies of eels from British waters are limited to three, all of which have been made by continental workers; 'Age and growth of some eels from a small Worcestershire pond', by Hornyold (1922); 'Age determination of eels from Norfolk and Cumberland', by Jespersen (1926) and the brief reference to the age of eels in the Severn and an Irish river (Clare?) by Marcus in 'Über Alter und Wachtum des Aales' (1919).

The present report, based on material collected from 1940 to 1944, deals with the age and growth of the yellow and the age of silver eels of the Windermere catchment area. The determination of the age of the eel is somewhat complicated, and information about it is much scattered throughout European literature. It has been thought, therefore, that a detailed account of the subject might be included with advantage in this report.

The eels examined came from both lake and river water (Fig. 1); the former represented by Windermere, the latter by the R. Leven which flows out of Windermere and the Cunsey Beck which, draining Esthwaite Water, flows into Windermere. All these waters are soft, the chemical characteristics expressed

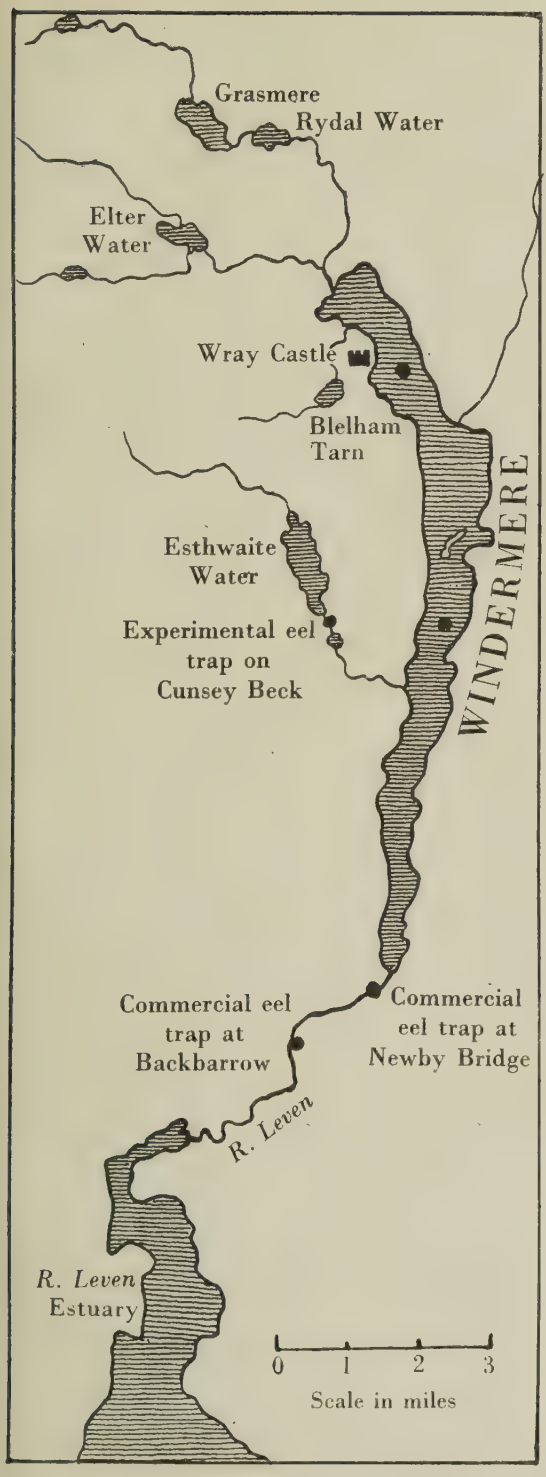


Fig. 1. Windermere catchment area, showing places mentioned in the text.

as salts in parts per million being briefly as follows: Windermere: $CaCO_3$ 8·5, iron 0·02, silica 1·6, nitrate 0·02, phosphate 0·002, *p*H 6·9; Esthwaite: $CaCO_3$ 15·5, iron 0·03, silica 1·7, nitrate 0·17, phosphate 0·003, *p*H 7·2.

In addition to the eel the fish to be found in Windermere are the salmon (*Salmo salar* L.), brown trout (*Salmo trutta* L.), char (*Salvelinus alpinus willugbii* (Günther)), pike (*Esox lucius* L.), perch (*Perca fluviatilis* L.), stickleback (*Gasterosteus aculeatus* L.), bullhead (*Cottus gobio* L.) and minnow (*Phoxinus phoxinus* (L.)). The R. Leven holds salmon, sea trout (*Salmo trutta* L.), pike, stone loach (*Nemacheilus barbatula* (L.)), stickleback, bullhead and minnow. The Cunsey Beck has the same species as the R. Leven except that salmon and sea trout are rare visitors.

The present report deals with the stages represented by the yellow and silver eels. Eels enter fresh water as glass eels or elvers, these fish being about 7–8 cm. long and probably about 2 years and 10 months old. The *yellow eel* is the name given to the fish during the period from its entrance into fresh water until its migration to the sea. This period, which is one of growing and feeding, may last for many years. The yellow eel has an olive green dorsal surface, and a yellowy white belly; the head is broad, the mouth wide and the eyes relatively small.* When growth in fresh water is completed such an eel becomes a *silver eel*, the stage which is ready to go to the sea for reproduction. The dorsal surface of the fish is now a bronzy black or dark brown and the belly milky white or silver. The head of the silver eel looks narrower and the snout more pointed than in the yellow eel and the eyes are definitely larger.

2. MATERIAL AND RECORDING METHODS

The material examined was captured by the following methods:

Yellow eels. The smaller specimens, locally called 'snigs', the length of which may be regarded as ranging roughly from 9 to 30 cm., were mostly taken by hand net from the Cunsey Beck or were caught in the trap there operated during the autumn for silver eels. The majority of the specimens were longer than this and came out of Windermere, most of them

* There is a general opinion among scientific investigators and practical fishermen that yellow eels show two forms, a broad-headed type which has a flat muscular head and thick lips (Breitkopf) and a narrow-headed type with more pointed head and thin lips (Schmalkopf). Continental workers who have examined morphometric data in order to establish whether or not the two forms constituted two races of eels have obtained inconclusive results. In the present investigation no distinction between broad- and narrow-headed forms has been made.

being caught in perch traps,* a few of them were taken in the Dutch eel (Fyke) net which is an unbaited set net, and a number were taken on long lines.

Silver eels. The majority of these were taken, as they migrated to the sea, in the experimental trap situated on the Cunsey Beck near its outflow from Esthwaite Water and operated by the Freshwater Biological Association. A few specimens came from the commercial traps on the R. Leven at Newby Bridge and Backbarrow.

Yellow eels were captured throughout the year; the time of capture of silver eels was conditioned by the autumn migration. In Table 1 the seasonal distribution of those eels examined for age is given.

Measurements

All the eels were measured in centimetres from the snout to the end of the caudal fin. The larger eels were measured in half-centimetre units which in some cases was done to the nearest half centimetre, in others to the half centimetre below; in order to make the measurements uniform the latter have been raised by 0·25 cm. Small specimens, that is those less than 30 cm. long, were measured to the nearest millimetre below. The individual eels were weighed, those of less than 1000 g. on a balance registering 10 g. units, specimens over this weight on one registering ounces, the latter weights being converted into grams for uniformity (28·35 g. = 1 ounce). The yellow eels ranged in length from 9·0 to 95 cm. and from 1 to 1785 g. in weight, and the silver eels from 35·5 to 97 cm. and from 65 to 2040 g.

Table 1. *The seasonal distribution of the eels examined for age*

(The silver eels examined from January to May were autumn-caught specimens which had been kept in captivity.*)

	No. of specimens examined												
Month ...	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Yellow eels	—	—	—	2	42	43	21	98	40	16	6	7	286
Silver eels*	1	64	3	2	3	—	—	34	82	58	17	11	275

Distinction between the sexes

The sex of the eel has been the subject of much interest, discussion and investigation, but some points about it are still obscure. There are no external sexual differences, and the separation of the sexes has to be done by the examination of the gonads. Even this does not allow a sure separation to be made if the eel is less than a certain size. It has been found that among silver eels two obviously different types of gonad are found: (1) in all specimens of over 50 cm. and in most of those over 40 cm. long the gonad is a wide crenulated ribbon-like structure, in which in some cases it is possible to see eggs with the naked eye; (2) in smaller specimens, usually those less than 40 cm. long, the gonad is a narrow, lobed or deeply scalloped piece of tissue; both types lie beneath the gut, are attached by their inner margins to the body wall, and extend from the region of the pectoral fins to the anus. The first structure is reasonably termed the ovary, the second is known as Syrski's organ. Syrski (1874) described the macroscopic and microscopic appearance of both types of structure, and found the eggs in the crenulated organ and thus established the female fish, and although he could not demonstrate sperms in the lobed organ he concluded from the presence of certain ducts and other anatomical details that this organ was the testis and therefore fish having a lobed organ were males.

These criteria for differentiating the sexes by macroscopic differences in the gonad although accepted in most work done on eels, including even some done on change of sex (Tesch, 1928), have, however, been questioned from time to time, criticism being concerned with the validity of regarding Syrski's organ (the lobed one) as a male gonad. It has been argued that this structure is an undifferentiated gonad and thus cannot be regarded as diagnostic of maleness. In the present investigation it has been assumed that those eels, silver and yellow, with the crenulated ribbon-like gonad are female, and those with a scalloped or lobed gonad (Syrski's organ) are male.

In yellow eels less than 21 cm. the gonad is an undifferentiated narrow strip of tissue. Most specimens between 21 and 25 cm. show a similar strip, but occasionally it is possible to recognize a suggestion of crenulation or scallops. In the majority of individuals between 25 and 28 cm. long the two types of gonad are developed to the extent of making possible the separation of male and female; the smallest male recognized was 27·5 cm. and the smallest female 22·7 cm. long. In all specimens over 28 cm. the crenulated and scalloped gonads are easily recognizable, and thus the sexes can be distinguished. The size of the fish may itself be an aid to sex distinction. Of the yellow eels examined during the investigation the largest male measured 48·5 cm. and the largest female 95 cm.; of the silver eels examined the largest male was 43·5 cm. long and the smallest 35·5 cm.,

* The war-time fishery for perch in Windermere by means of unbaited wire traps lasts from mid-April to the end of June; for scientific purposes some of the traps were left in the lake during the rest of the year. Eels, in varying numbers, entered the traps at all times of the year.

whereas the largest female measured 97·0 cm. and the smallest 47·0 cm. In connexion with this last fact it must be recorded that smaller female silver eels do occur in the Windermere catchment area, for, since the close of this investigation, four such fish have been captured, two at the trap at Cunsey Beck, 44·5 and 45·6 cm. long, and two others 44·5 and 44·0 cm. at the Backbarrow eel traps. Female silver eels of this size are rare, a phenomenon supported by evidence from European waters.* Thus in the Windermere catchment area it appears that yellow and silver eels of 50 cm. and more in length are females, and any silver eels less than 50 cm. long are, with few exceptions, male.

The sex of the majority of the eels used for age determinations was established by internal examination; in those cases where this was not done it was usually possible to distinguish male from female fish by length. The latter criterion was also used to separate the sexes when examining the eel for length data only.

Age determinations

The age of the eel may be determined from the otoliths, scales, opercular bone and vertebrae. The first two provide the most satisfactory material and have been used in this investigation. In most cases age determinations have been made from the otoliths in conjunction with the scales and in a very few instances from the scales alone. In all over 300 yellow eels and the same number of silvers were examined for age, and of these 286 of the yellow eels and 275 of the silver eels gave results which it was possible to use. Of the 286 yellow eels the age of 87 was determined from the otoliths alone, of 168 from otoliths in conjunction with the scales, and of 16 from scales only; of the 275 silver eels, the age of 175, 96 and 4 specimens was determined by the three methods respectively.

3. METHODS OF ANALYSIS

The use of otoliths or scales or both for determining the age of eels involves certain matters of technique, and their interpretation in terms of age needs some explanation. It has been thought advisable therefore to go into the subject in some detail.

(*a*) *The otoliths*

An eel otolith is approximately bean-shaped and has a concave and a convex surface, the latter having a ridge down the centre. It varies with the size of the eel; that from a silver eel of average length, one of 50–60 cm., would measure about 3 mm. down the long axis and down the short axis 2 mm. The otoliths—there are two, one on each side of the head—lie in the auditory capsules. A cut from the neck towards the snout which lifts off the top of the skull exposes the brain, and the otoliths can then be picked out of the capsules on either side of it. On removal they are cleaned by a brief immersion in absolute alcohol and then transferred for preservation to a tube of normal saline to which a little lysol has been added.

Prior to being examined for age the otoliths are soaked in creosote for at least 24 hr. The treatment is sufficient to make a few of them, usually those of younger eels, readable, but the majority need further preparation before the growth rings are visible. A technique for preparing the eel otolith for reading is described by Wundsch (1916) and Hornyold (1922). After experimenting with various methods a modified form of the latter's was adopted. The otolith, after being cleared in creosote, is dipped for a second or so in absolute alcohol, and then with the finger on the concave side its convex surface is rubbed on a fine carborundum stone. During this process it is examined from time to time in creosote by reflected light under the binocular and the rubbing is continued until the growth rings can be seen at their best; in some cases a brief immersion in very dilute hydrochloric acid will bring up the rings more clearly.

The otolith, when seen by reflected light against a dark ground, shows alternating light and dark concentric zones; the former are whitish and opaque and were laid down in the summer, the latter are darker and comparatively translucent and represent the winter growth (Pl. 2). The interpretation of such zones as annual and thus as records of the age of the eel has been justified by the experiments of Ehrenbaum & Marukawa (1913) who took glass eels and kept them in aquaria from 1 to 5 years. They found that the zoning on the otoliths of such eels, with few exceptions, registered the number of summers and winters of captivity.

The features presented by an otolith for reading are shown, somewhat diagrammatically for clarity, in Fig. 2. Their interpretation is as follows: there is a central darkly translucent area, which probably represents the first year of life, next to this a white opaque ring which is followed by a dark translucent one, indicating respectively a summer and winter, most likely of the second year of life; an otolith of an elver captured on its entrance into the river in the spring has this appearance and the zones on it are referred to as the 'sea-water rings'. Following this formation is a white opaque zone, the first zone recorded in fresh water and laid down in the first summer there; then following this is a dark translucent ring which formed during the first winter in fresh water; the subsequent alternating opaque and translucent rings mark the summers and winters of the successive years in the fresh-water life of the eel. It will be seen from Fig. 2 that five summers and four winters have been passed in fresh water, the edge

* In contrast to this Hornyold's data (1930) show that the mean length of the majority of the female silver eels of the Lac de Tunis in North Africa is below 50 cm.

of the otolith being bounded by the fifth summer band. The photographs show the actual features presented and their interpretation in terms of age.

It is difficult to determine exactly at what time of year the summer and winter zones are laid down, a difficulty which is increased by the fact that at the beginning of their formation the two zones are not clearly separated. Marcus (1919) found that no summer growth was apparent in April, May, June, July and August according to the river from which the eels came, and had only proof of the origin of such growth in September and October. He notes that by November summer growth of the otolith is ended and the material of the winter ring is already being formed. In the Windermere specimens no

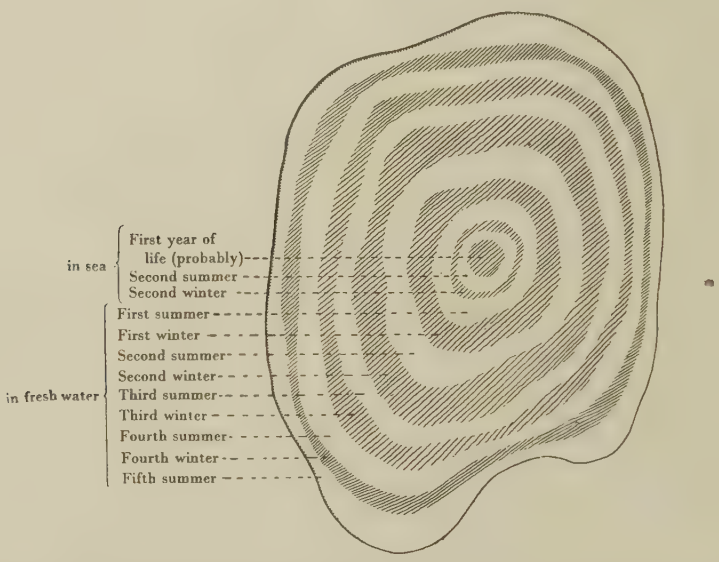


Fig. 2. Diagram of an eel otolith to show the features presented and their interpretation in terms of age (see text, page 29). Otolith examined by reflected light shows summer zones as white and opaque areas (white in diagram) and winter zones as dark and translucent (cross-lined in diagram).

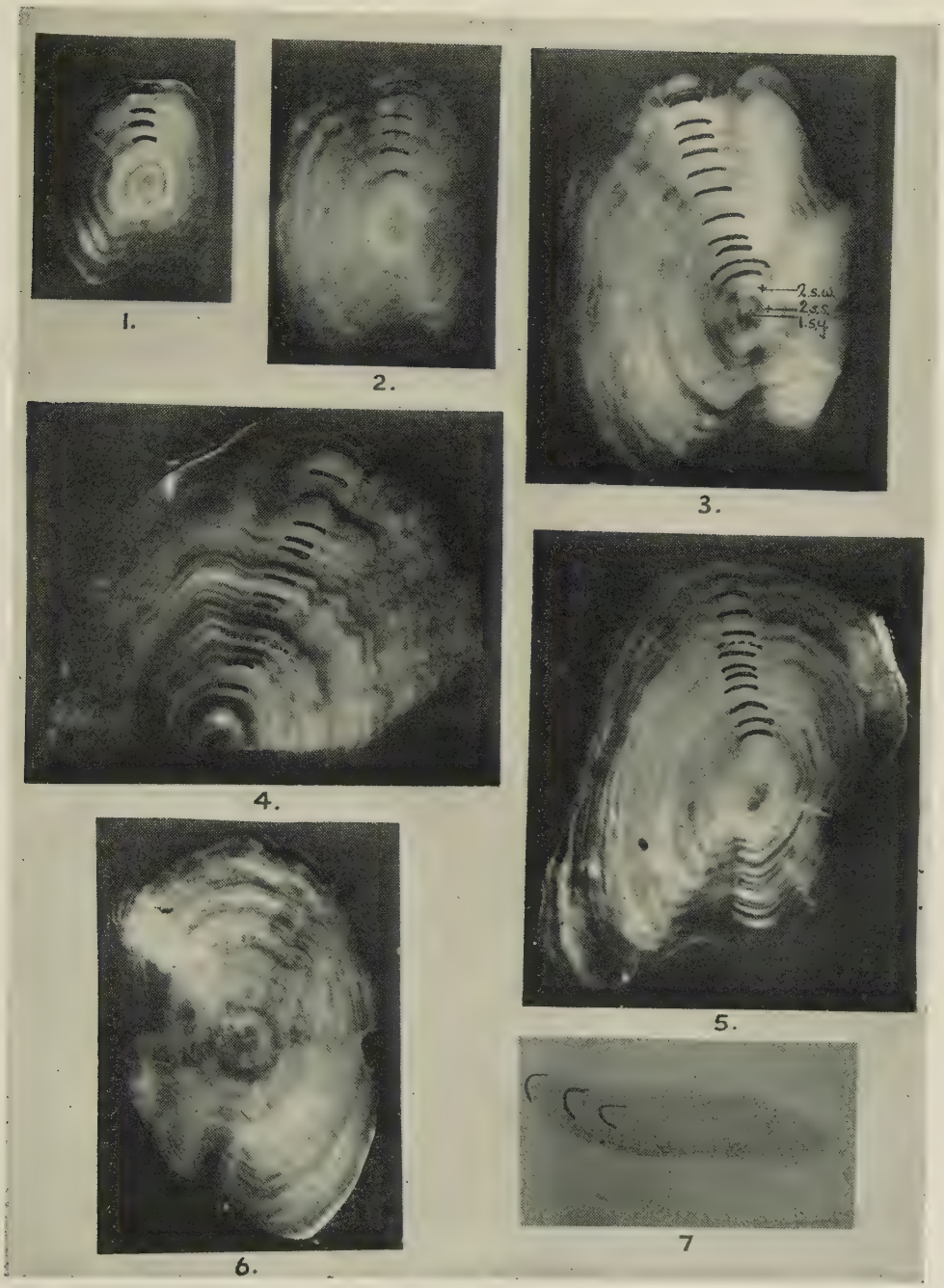
summer zone can be distinguished at the edge of the otolith until August, and it appears to be completed by the end of November.

In reading the age of the eel from the otolith it is usual to ignore the sea-water rings, the reading beginning with the eel's entrance into fresh water, and the record of the age, whether in years or in age groups, refers to the time spent in fresh water and not to the total life; this practice has been followed here.

The years of life (in fresh water) are usually recorded in terms of age groups, O group, I group and so on. In this report the method used in recording the age of marine fish, namely, that by which a fish during its first year of life belongs to the O group, during its second year of life to the I group and so on, has been adopted. The elver enters the Windermere catchment area, via the R. Leven, in the spring, in April and in early May, and therefore all those eels which are in their first year in fresh water reckoned from that spring until the following one are classified as O group, those which were in their second year reckoned from spring to spring were put into the I group, and so on. The date of the spring has been fixed as 1 May, so that eels caught after this date have entered a new year group.

Since the eels were caught at all times of the year (Table 1) the age-group index (I, II, etc.) covers two things: the year of life, i.e. X group means that the fish is in its eleventh year of life considered from spring to spring, and (2) the actual growing period of the eel during that eleventh year; this is practically confined to the months of May to September-October, inclusive.

Eels were caught at all times of the year. The assignment to an age group of an eel in (say) the tenth year of its life in fresh water depends on the time of year when it was caught. The period of growth during any year is practically confined to the period May to October, but the time when an eel enters upon another year of its life in fresh water has been fixed as 1 May. An eel caught in March or April at the close of its tenth year, for example, will have laid down its eleventh winter zone but it will still be placed in the X group because it has not yet passed the date for entering upon the next year of its life. An eel caught in May of the same year and showing the same number of winter zones will be placed in the XI group. This method of assigning the age



Photos 1–7. Photographs of eel otoliths. (See p. 29 and Fig. 2). The marks in photos 1–5 indicate the winters in fresh water; in photo 3 the two sea years are pointed out. 1. Four winters, fifth summer at edge. Eel 18·5 cm. 2. Six winters, seventh summer at edge. Eel 33·0 cm. 3. 12 winters, edge forming the last one. Eel 49·5 cm. Sea life shown by 1 *s.y.*=1st sea year, 2 *s.s.*=2nd sea summer, 2 *s.w.*=2nd sea winter; opaque white zone following 2 *s.w.*, is first summer in fresh water. 4. 16 or 18 winters, last one at edge. Eel 80·5 cm. 5. 12 or 13 winters, last one at edge. Eel 53·0 cm. 6. Winter and summer zones of the 'multiple band' type (see p. 31). 7. Scale showing three annual zones.

group has not weighted the results referring to the age and length relationship of yellow eels, since if mid-July is taken as the middle of the growing period it will be seen that (Table 1) as many eels were taken before as after this time; thus the X group refers to a fish of 10+ years old. The silver eels, however, were captured in the autumn when ready to migrate, a time when, presumably, growth for the current year is completed, and therefore the length figure given for the X group will represent the length achieved at the end of the eleventh year of life, the fish being 11 years old as far as growth is concerned. Thus there is some weighting of the age data in silver eels.

Ehrenbaum & Marukawa (1913) also followed the convention of classifying eels in their first, second year of life as O group, I group, etc., and took the year as beginning in the spring, but since all their material was caught in the winter the close of the year of life period (spring to spring) coincides to all intents and purposes with the close of the growth period itself. Thus the length given as achieved by, for example, the I group will denote that achieved at the end of the second year of life, not during it, and the otolith from such an eel will show two winter bands, the second being at the edge of the otolith.

The time covered by the age-group index (I, II, etc.) is not, however, always that usually accepted by fishery workers. Marcus (1919) points out that if the time of death is unknown it is impossible to tell it from the breadth of the summer zone in formation since that may not appear before September; as a result one cannot be sure if the eel has passed from one year of life into the next (judged from spring to spring), and thus one might put an eel in the II group that should be in the I group. Therefore in allocating the year class he has decided to go back to the last completely formed winter ring and to give the age only according to the closed group; thus if he investigates an eel in August which is $4\frac{1}{2}$ years old it ought to be in the IV group (being in its fourth year), but when the completed winter bands only are counted it becomes III group. Wundsch (1916) and Tesch (1928) have followed Marcus's method of age grouping. It will be realized that in comparing the results of these writers with those obtained from Windermere the actual age in years signified by the group will differ by at least one whole year; attention, however, has been drawn to this when any such comparisons are made.

The use of otoliths as a means for determining the age of the eel presents certain difficulties. The grinding of them takes an appreciable time, and during the process they can very easily be broken and this may render them useless. Because of its friable nature it is seldom that the edge of the otolith can be finely ground, and thus the growth zones in the thicker perimeter are not well defined and a year's record may easily be missed. The interpretation of what is seen is often by no means easy nor is the result reliable; for example, in the 'multiple-band' zone type, where there are several very narrowly separated zones, it is difficult to determine whether each represents a distinct summer or winter zone or if collectively they form one (Pl. 2, photo 6). The summer and winter zones are seldom shown with diagrammatic clarity even in young eels, and as the fish gets older the zones get closer so that it is difficult to dissociate the several years from each other. In view of this latter difficulty continental workers are agreed that, on the whole, the otoliths of eels showing more than 7 or 8 years, specimens usually 35–40 cm. long, are more or less unreadable and thus of little value for age determination. The majority of the fish which I examined were over 40 cm. long, but an attempt has been made to read them in spite of the likelihood of error in the results obtained. It is probable that an age reading of between 8 and 12 years may be out by plus or minus 1 year and readings greater than this by a similar error of 2 years.

(*b*) *The scales*

The scales of an eel are flat, oval objects about 2·2–3·2 mm. long in a medium-sized fish (55 cm.) embedded in the skin. They cover the body and may or may not overlap each other. Their arrangement may vary somewhat: above and below the lateral line near the anus they lie so that some of them are oblique to the long axis of the body with others grouped at right angles to them, the effect being somewhat like parquet flooring (Fig. 3). To obtain scales for the age determinations a piece of skin about 2 in. long was cut off both sides of the body from the region just in front of the anus and above the lateral line; the preservation of this in 5% neutral formalin ensured that the scales were flat when examined later. When needed for examination the scales were scraped off the skin and shaken in a little water and methylene blue to clean and stain them; from these a random sample of well-shaped ones was taken of which ten, at least, were read under the microscope with a magnification of about 100 (Hornyold (1931) describes a slightly different technique).

The structure of the scale is distinctive (Pl. 2, photo 7 and Fig. 4). It has been usual to think of it as consisting of a fibrous ground substance, smooth on one side (that nearest the body) and bearing many calcareous knobs or platelets on the other. Waly (no date), however, in a recent investigation has shown, by sectioning, that the scale is composed of loculi, round, oval, or polygonal in shape. He states: 'Each loculus is formed of closely allied fibres, with intercommunicating delicate threads coursing from the external to the internal surface of the scale. The colorability of the loculus is due to the presence of numerous very fine particles of a calcium salt (probably a phosphate) scattered in this region in and

Fig. 3. The arrangement of the scales: (*a*) piece of skin taken from above lateral line and just in front of anus of 27 cm. eel; (*b*) the same from 47 cm. eel.

Fig. 4. An eel scale showing five annual zones. Each zone consists of several rows of calcareous 'platelets' arranged in concentric rings. The zones are divided from each other by a narrow band of fibrous ground substance (width of this band a little exaggerated).

between the fibres.' These loculi, previously regarded as platelets, are arranged in rows which are more or less parallel to the margin of the scale and they themselves are grouped into concentric zones, these zones being divided from each other by a narrow band of fibrous tissue (Fig. 4).

As Gemzöe (1908) notes, this zoning arrangement led Baudelot (1873), Petersen (1894) and Stuart Thomson (1904) to suspect that there was some relationship between the form of the scale and the growth of the eel. It was, however, Gemzöe who established that the zones were annual in character, a fact which he had suspected when comparing the scales of the cod with those of the eel. He knew that the life of the eel is marked by periods of activity and growth alternating with periods of quiescence and little or no growth, roughly coinciding with summer and winter, and by following the growth of the scale he found that the larger calcareous platelets of the zone were laid down during the growing period and that these became smaller towards the edge of the zone and finally ceased altogether during the period of little or no growth. The absence of platelets caused the rest to be framed in a ring of uncalcified fibrous tissue (Fig. 4). (The term platelets will be used since this is the terminology of previous workers.)

The month when the platelets are formed varies. Gemzöe found that the scales began to form by the end of June and formation was practically finished by the end of August. Ehrenbaum & Marukawa (1913) found much the same thing, noting, however, that in the yellow eels the scales were still growing at the end of September. Both they and Gemzöe point out that silver eels complete the year's growth of their scales before the yellow eels do so. The investigations of Marcus (1919) showed that the time of appearance of the new growth varied with different waters; but he regarded growth as ended by October or November. In eels from Windermere scales showing new growth at their edges have been found in July, August and September. It seems likely that scale growth is ended by October, but, since I found some difficulty in determining the growing edge, information on this point is somewhat inconclusive.

Although it has been shown that the zones on the scale are annual in character, the determination of the age of the eel from the scale is not a simple matter of reading these zones. In interpreting the scale in terms of age it is necessary to realize that: (1) length and not age determines the time of appearance of scales, (2) scales from any one fish do not all show the same number of annual zones, (3) there is the possibility that the scale may fail to record an annual zone.

(*c*) *Discussion*

Length and not age determines the time of appearance of scales. Gemzöe, deducing the age of the eel from length measurements, concluded that scales were assumed after the eel had been 2 years in fresh water, namely, during its third year there, and thus to obtain the time spent in fresh water 2 years must be added to the scale reading.

Ehrenbaum & Marukawa (1913) and Marcus (1919) questioned not only this conclusion but the idea that the assumption of scales was a thing which was associated with the fish having reached a certain age. They showed that the time of appearance of the scales depends not upon the age of the fish but upon its length. Ehrenbaum & Marukawa (1913) kept elvers in aquaria and at the end of 4 years examined the eels, which registered 4 years on the otolith, for scales. Out of 23 eels only 8, which ranged in length from 18 to 24 cm., had assumed scales, 14 individuals from 9 to 18 cm. long had no scales and one of 28 cm. recorded two annual zones on its scale. This and other experiments led Ehrenbaum & Marukawa to conclude that the eel having attained a certain length, approximately 16–20 cm. (termed by Tesch (1928) the 'scale size'), put on its scales regardless of its age. These workers and others have found that 'scale size' is usually reached during the fourth year in fresh water, but it is also attained during the second, third, fifth or even sixth year. Thus to obtain the age of an eel from its scales anything from 1 to 5 years, usually 3, may have to be added to the number of years recorded on the scales, and Gemzöe's statement that 2 years must always be added is proved incorrect.

Evidence as to the age when 'scale size' is reached is obtained from eels which provide readings of both otolith and scale from the same fish, the difference between the two readings giving the age when the scales were assumed. A generalized figure for this age may be reckoned from sufficient examples of these 'differences', a figure which represents the number of years which must be added to the scale reading to find the age of the eel from the scale.

In the present investigation 310 eels provided both scale and otolith data, and from these the age at which scales were assumed was deduced. It was found that the difference between the otolith and scale reading ranged from 1 to 5 years, scale assumption would therefore occur during the eel's second, third, fourth, fifth or sixth year in fresh water. The percentage proportions of these several years was 13, 27, 38, 16 and 6% respectively. These percentages have, without doubt, been affected by the fact that the 'difference' data were obtained in most cases from older eels, and the otolith reading in such eels is liable to error. This probably accounts, to some extent, for the fourth year not being so predominantly the scale year as is found by other workers. These percentages were taken into account when adding the number of years (the difference figure) to the scale reading in those age determinations based on the scale only.

Scales from any one fish do not all show the same number of annual zones. The determination of the age from scales is complicated by the fact that the

scales of any one eel do not register the same number of zones. The number may vary both from place to place on the body and among those from any one area on the body. This is apparent from Table 2, which gives results obtained from a Windermere eel

Table 2. *Results of scale readings from nine places on a 69 cm. eel showing the frequency of occurrence of the different numbers of zones at each place*

No. of annual zones	Place								
	1	2	3	4	5	6	7	8	9
5	4	—	—	—	—	—		—	—
6	4	—	—	—	—	—	1	—	—
7	4	—	—	—	—	—	1	4	—
8	4	4	6	2	2	—	11	6	—
9	4	6	1	2	5	1	6	9	6
10	—	2	1	5	5	6	1	1	7
11	—	6	8	5	4	10	—	—	5
12	—	1	2	3	1	2	—	—	1
13	—	1	2	3	3	1	—	—	1

69 cm. long. A sample of 20 scales examined from nine different places on this eel's body (Fig. 5) showed that (1) the scales gave readings varying from 5 to 13 zones, (2) the proportion of scales with maximum number of zones was not the same at each place, and (3) the scales taken from places 4 and 5 had the greatest proportion of scales showing the maximum number (13) of zones. This last fact affects the choice of scale for reading, since the scale with the maximum number of zones implies the oldest one, and therefore the one required for use in age determination. The area where such a scale is most likely to occur is apparently in places 4 and 5 of Fig. 5. In this investigation scales were taken from place 4, but it will be evident from the low proportion of those with maximum zones that, in the routine examination of ten scales per fish, there is the likelihood of the one having the most zones being missed. Records of the ten readings made have been noted, and statistical treatment of these data might establish the degree of probability of occurrence of the scale with maximum zones.

In connexion with the variation in the number of annual zones recorded by scales on one fish it became evident from the measurements of scales that there was no relationship between the number of the zones present and the actual length of the scale; for example, a scale measuring 3·0 mm. may record ten rings, whereas one of 3·5 may have only eight and vice versa. This point is significant when back calculation of growth from the scale is considered.

The possibility that the scale may fail to record an annual zone. The possibility that the scale may fail to record an annual zone has to be considered when scales are used for determining the age of the eel. This possibility was suggested to Marcus (1919, p. 22) by the fact that in eels of poor growth there is 'an increase of the difference between the otolith and scale rings with increasing age'; his table demonstrating this is given here as Table 3. Further, he suggests how the suppression of an annual zone has come about. It has been noticed that on eels of almost any size scales may occur which show incomplete annual zones. These zones may be various in form ranging from an almost complete annual ring to a fragmentary portion at the end of the long axis; some of the forms are shown in Fig. 6; they are all called 'caps'. Concerning these caps Marcus says: 'In the continuation (Fortschreiten) of this process (i.e. cap formation) new ring formation stops entirely.

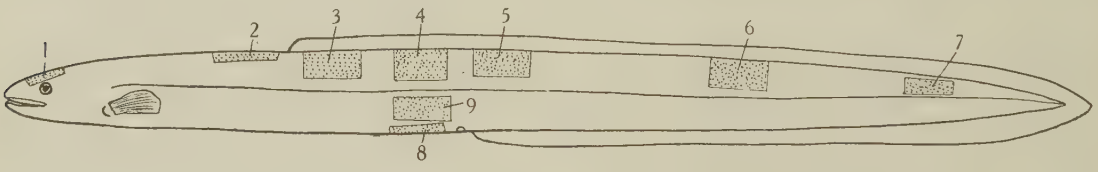


Fig. 5. The eel, 69 cm. long, showing the nine different places from each of which a sample of 20 scales was taken for examination (see Table 2).

Table 3. *Marcus's* (1919, *p.* 22) *table showing the increase of the difference between otolith and scale rings with increasing age*

Difference between otolith and scale rings	Completed age-groups							
	Male		Female					
	V	VI	IV	V	VI	VII	VIII	IX
3	2	1	2	12	6	—	—	—
4	10	4	—	7	70	37	5	—
5	—	5	—	1	1	13	7	3
Total	12	10	2	20	77	50	12	3

Legend to Fig. 6.

Fig. 6. Scales with incomplete annual zones, 'caps' (cap is stippled). The reading of the caps in terms of annual zones is shown by the figures on the scale, the number of annual zones presented by each scale being as follows: (*a*) scale without caps 3, (*b*) 6, (*c*) 7, (*d*) 10, (*e*) 10, (*f*) 9, (*g*) 11 and (*h*) 11.

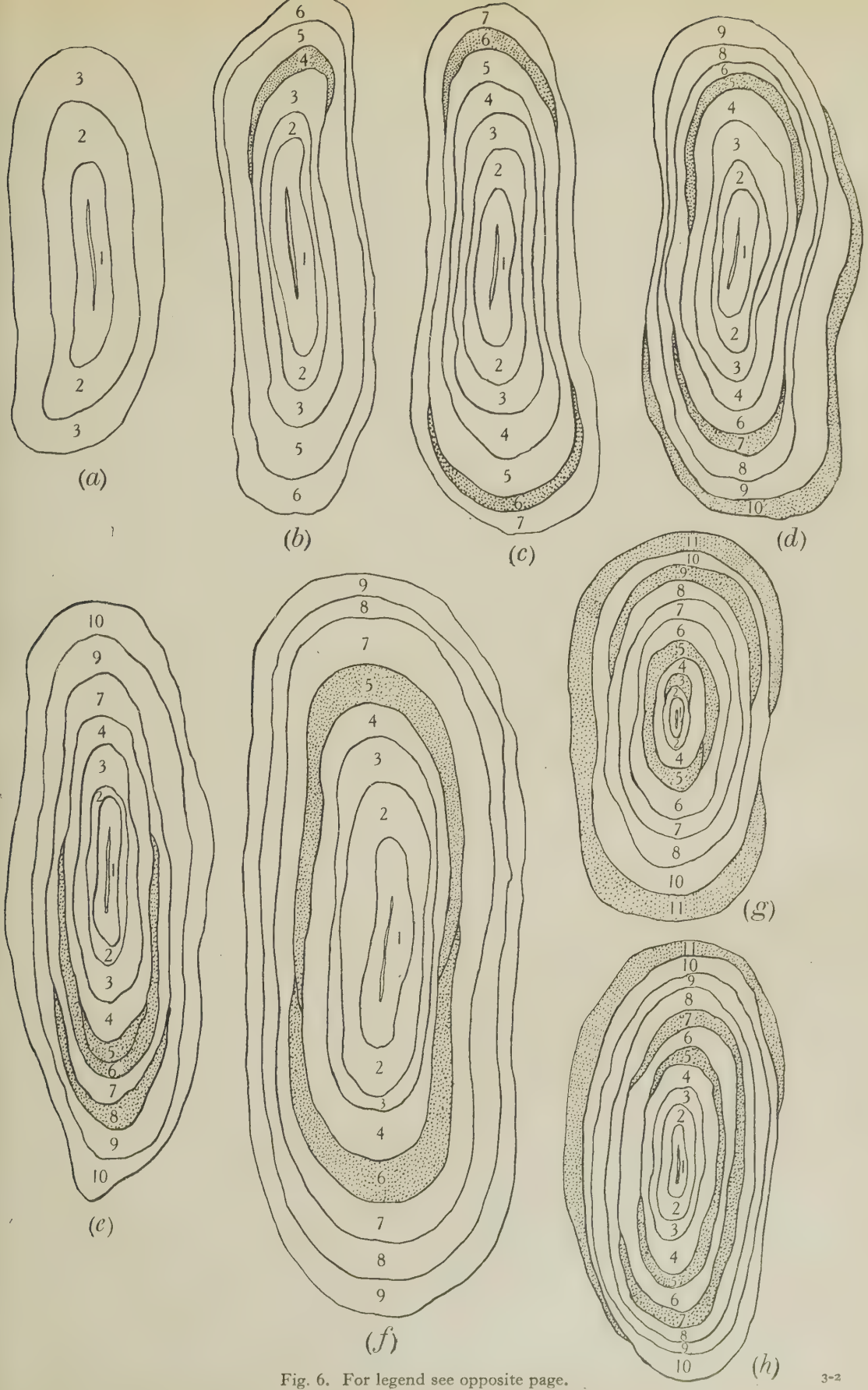


Fig. 6. For legend see opposite page.

Cap formation does not occur at the same time on all scales, but in one year in some and in the following year in others so that always there are fewer scales with the right number of rings, thus gradually there is a diminution of ring numbers which is progressive.'

Thus to Marcus the cap is a stage to final suppression of the annual zone, and the postulation of a missing zone is the explanation of that increase of the difference between otolith and scale reading found with increasing age. This phenomenon he finds characteristic of eels which show poor growth, because slow growth will increase the chances of missing a zone, since it gives a greater number of years during which suppression of zones can take place.

Caps on scales are also noted by Ehrenbaum & Marukawa (1913), Hornyold (1922, 1930) and Gemzöe (1908), but none of them attach any significance to them, and in evaluating them they merely note that a cap at both ends counts as one year, or alternate caps as two separate years; they do not figure any of the many varieties of caps which may occur or indicate how such would be interpreted. A cap at each end of the long axis of the scale certainly suggests that it constitutes an aborted annual ring, and if this particular form is so accepted, then other forms must be interpreted in the same way; therefore in this paper, caps, whatever their form, have been counted as annual rings. Some of the main types encountered in the present investigation, with their interpretation in growth years, are given in Fig. 6. In many cases capped scales were those giving the maximum age reading, and it was necessary therefore to examine them carefully and read them aright.

It is not unlikely that the caps may be a result of the relationship between the body surface of the eel and the rate of growth of the fish. If so, the cap might suffice to cover the small increase of surface made during a year of slow growth, whereas if growth is rapid and therefore the increase of surface area large, a cap might be put on to cover this increase in addition to the covering supplied by the complete concentric annual zone. In the former case the cap represents and counts as a year's growth, in the latter this is not so.

The age and growth rate of most fishes are obtained by back calculation from their scales; Hornyold (1929) has applied this method to eel scales. In the present investigation several eels of various lengths were taken and ten scales from each fish were measured and the number of annual zones on each of the ten noted. It was found that in many cases the larger scales had fewer rings than the smaller ones, indicating that scales recording a younger age had grown more quickly than those showing an older one. In view of this evidence it was considered that they were unreliable for back calculation and Mr H. J. B.-Wollaston thought it was unnecessary to submit them to further tests for this purpose.

(*Conclusion to follow*)

CANADIAN ARCTIC WILD LIFE ENQUIRY, 1942–43*

By HELEN CHITTY and DENNIS CHITTY, *Bureau of Animal Population, Oxford University*

(With 4 Figures in the Text)

1. LEMMINGS

1942–43 was the second year of scarcity (following a peak) in the lemmings at the majority of places in northern Quebec and northern Baffin Island (groups 2 and 7). In the former area 'mice' were also said to be scarce although they had been abundant during September and October at Georges River. An observer at Pond Inlet, northern Baffin Island, anticipated increasing abundance in 1943–44 as there had been a slight recovery in the spring of 1943.

Lemmings had crashed at River Clyde and in central and southern Baffin Island (group 6) during 1942–43, one year later than in the far northern part of the island and four years after the last crash in all these areas. (The course of the cycles from 1935–40 is summarized in an earlier paper (1).)

All observers in the southern part of Hudson Bay and James Bay areas (group 3) indicated a scarcity of small rodents. As there were no reports of *increase* or abundance in lemmings or 'mice', a situation similar to that of 1938–39, it seems likely that 1941–42 had been a peak 'mouse' year in this area and that here too there had been a four-year cycle.

Lemmings were still scarce on the coast in group 4 (west coast of Hudson Bay) but inland, particularly around Padlei and Baker Lake, *increase* was reported. Since increasing abundance was also observed at Eskimo Point and Chesterfield Inlet in the spring of 1943, it is probable that recovery had begun in this area.

A decrease was reported on Southampton Island for the first time since 1936–37 and at Repulse Bay the previous year's decrease had continued.

There was a third year of increase in lemmings on the islands of the Western Arctic (group 8) and *increase* was also reported at Bathurst Inlet (group 9). 1942–43 may have been the peak year, as at Cambridge Bay numerous lemmings still in their fall coats were found dead on the ice in the spring of 1943 and they were said to have been scarce on the mainland and Kent Peninsula south of this post.

It is impossible to decide what was happening to the lemming population north of Great Slave Lake (group 10) as the picture in this region has always been obscure. From Coppermine to the Mackenzie River delta (group 11) lemmings continued to be scarce.

2. ARCTIC FOX

Broadly speaking, arctic foxes decreased throughout the Eastern Arctic during 1942–43 while still increasing in the western part of their range.

A year after the disappearance of lemmings from northern Quebec there was a crash in foxes in 1942–43 although they had been abundant at Georges River from September to November, and in May 1943 there were some signs of recovery at Fort Chimo and Payne Bay. A similar crash might have been expected in northern Baffin Island where the lemmings had also disappeared in 1941–42; but observers noted little change in numbers and suggested some reasons for this.

Pond Inlet. 'White fox in this sector in the early fall were exceptionally scarce, and the first two weeks of the trapping season very few were caught. However, around the 1st December the foxes started coming around and from then onwards until the end of the trapping season natives' trapping activities were fair. At no time during the outfit was there any great migration or "run" of foxes in this vicinity although in December we experienced a small migration coming from a northerly direction and heading south. This migration lasted for about two weeks. In March we heard of a great migratory move in the Lancaster Sound district, but unfortunately it never came down far enough to enter our trapping territories. Arctic hare, lemmings and white owls during the outfit were very scarce. But this spring, however, an increase in the number of lemmings was observed. As lemming breed very fast we are expecting them to be very plentiful next outfit.' (A. T. Swaffield.)

39. *Pond Inlet.* 'There appeared to be no change in the numbers of foxes in this district from that of the previous year. In December 1942 there were a few foxes migrating south through Navy Board Inlet to the mainland of Baffin Island. Eskimos from the north end of Navy Board reported that these were a few local foxes wandering south in search of better feeding ground.' (H. A. McBeth.)

Arctic Bay. 'Fox returns are higher than in Outfit 272 [1941–42] but from the information we can gather from the natives there was little or no change in the number around and, if anything, foxes were more numerous in Outfit 272 than in Outfit 273. The increase in returns is attributed to better weather during the trapping season and to the fact that the natives were better off for country

* Promoted by the Northwest Territories Administration of the Canadian Government, Ottawa.

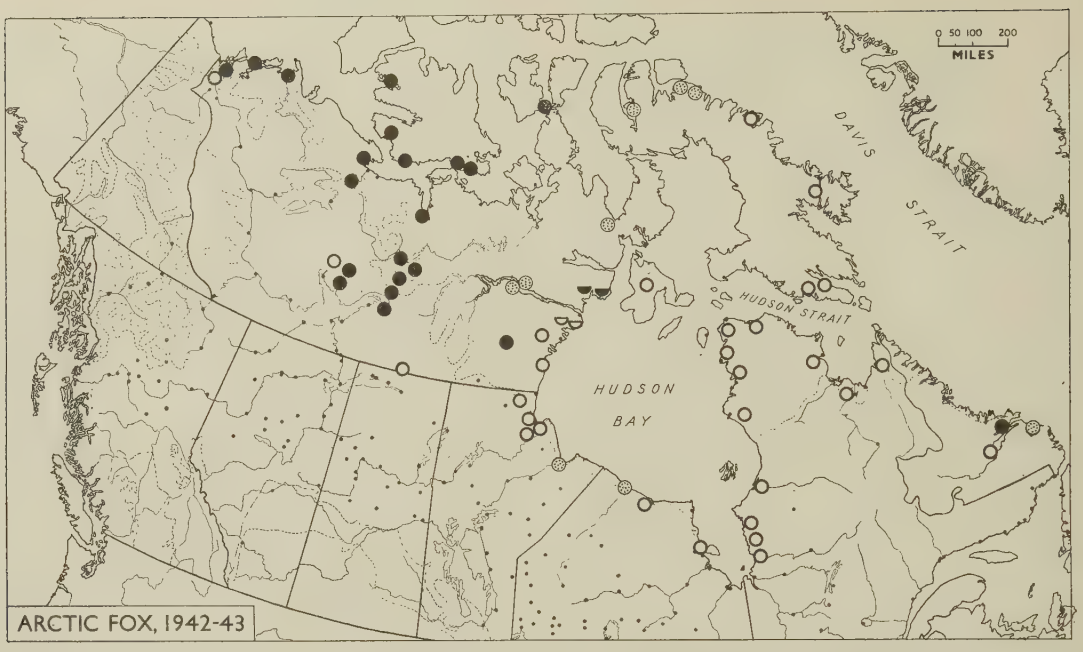


Fig. 1. Reports about the arctic fox population in 1942–43 compared with 1941–42. Each symbol is at the approximate centre of one observer's area: solid black disks are INCREASE; plain circles DECREASE; circles with small dots NO CHANGE, NOT ABUNDANT. Other black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones. (For explanation of the semi-circles see p. 43.)

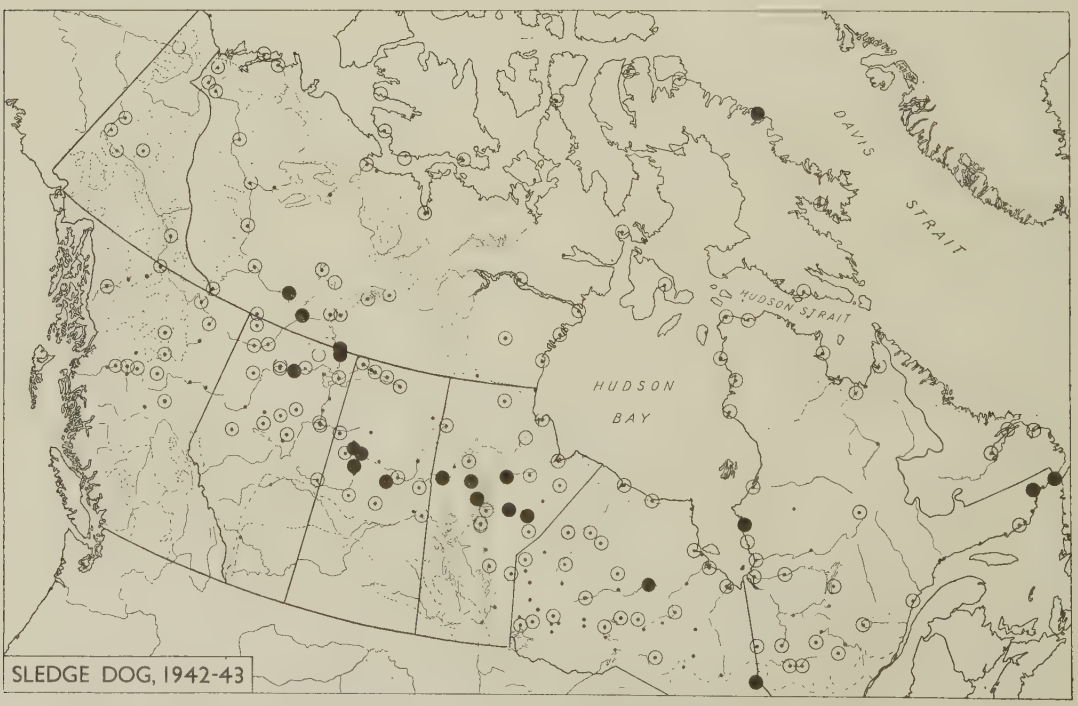


Fig. 2. Prevalence of disease among sledge dogs in 1942–43. Reports of disease, mostly serious, are shown by solid black disks; disease entirely absent by plain circles; other reports by broken circles.

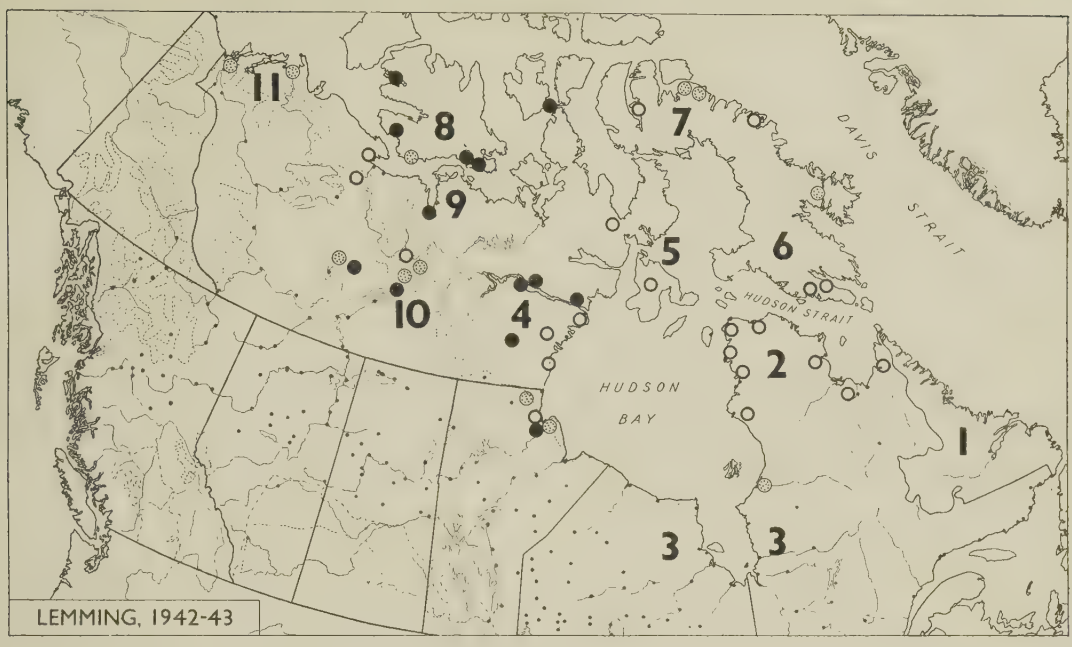


Fig. 3.

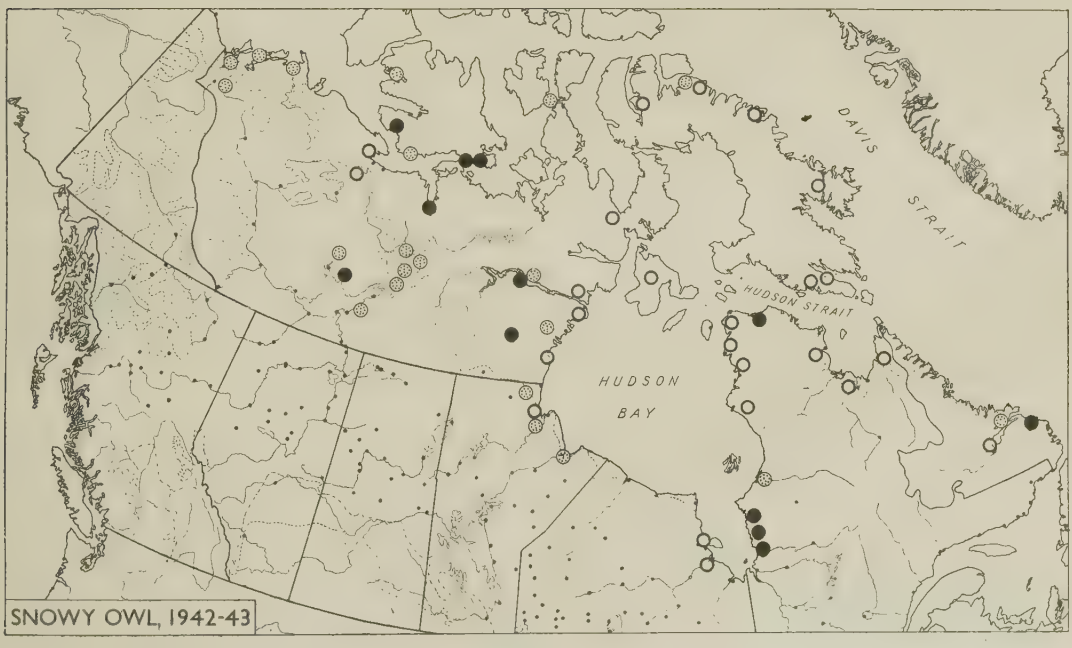


Fig. 4.

Figs. 3, 4. Reports about the lemming and snowy owl populations in 1942–43 compared with 1941–42. Symbols as in Fig. 1. Numbers show groups used in Tables 1 and 2.

food and in consequence were able to devote more time to trapping. We have noticed in this locality that practically all the trapping is done along the shore and on the sea ice and that foxes are reported to be very scarce on the land, whereas in south Baffin Island the majority of the foxes caught are trapped inland. The only feasible reason we can give for this difference is that seals are more plentiful here, thus enabling the natives to put up more catches which keep the foxes on the coast; also the bears are fairly numerous along our shores and the foxes hang around the bears and share their kills. If our deductions are correct, then it would appear that foxes in this area do not depend on lemming as a means of subsistence to the same extent that they do in the south. This would also explain why returns do not fluctuate so much at the most northerly posts as they do in the south.' (J. Bell.)

Foxes crashed in southern Baffin Island, and around southern Hudson Bay and James Bay along with lemmings and 'mice'. 1941–42 was, therefore, the peak year for arctic foxes in these regions as well as in northern Quebec, the last peak being in 1937–38, four years previous.

During 1942–43 foxes had become scarce on Southampton Island, but the report from Repulse Bay of *no change, neither abundant nor scarce* makes it difficult to say what was happening in this area since abundance had been reported for the year before.

1942–43 was the second year of decrease on the west coast of Hudson Bay. Foxes were still scarce on the coast south of Chesterfield Inlet but *increase* was reported at Padlei and between Chesterfield Inlet and Wager Bay, and a report from Baker Lake stated that the Back River natives observed more fox signs in the spring than fall, tracks heading north. As lemmings had already increased in these localities, it seems possible that further recovery may have occurred in this group during 1943–44.

Arctic foxes were abundant throughout the Western Arctic where *increase* was reported for the third successive year. There are indications that 1942–43 may have been the peak year (the last peak was reached in 1938–39), as some observers reported a decline in numbers in January 1943, particularly north-east of Great Slave Lake and on the mainland south of Cambridge Bay.

20. *Fort Reliance*. 'The trappers north of Clinton Colden and Aylmer Lakes state that in the early part of the winter, November and December, the foxes were very thick, but started to drop off at the beginning of January, although they were still abundant throughout the whole trapping season. The trappers to the east of Reliance, around the Thelon River, state that there was an average run of foxes in the early part of the season, but that they dropped off very rapidly in January. Three of the trappers stopped trapping in February because of the lack of fur.' (H. M. Silver.)

17. *Ptarmigan Lake and Clinton Colden Lake*. 'Arctic fox abundant in early winter, declined in numbers after Christmas.' (A. J. Knox.)

Cambridge Bay. 'Lemming migrated about November 1 in an easterly direction. Fox caught up to Christmas were very fat, from then on their condition dwindled to end of season. From native reports lemming and fox signs were very scarce on the mainland.' (E. J. Gall.)

30. *Cambridge Bay*. 'Arctic fox very abundant all winter, reported by hunters to have been exceptionally fat during the early part of the winter and in poor condition in the spring. The spring condition was reported as being touched by mange and skin eruptions in the form of boils. Abundancy of arctic fox appeared to be confined to the Arctic Islands, very few reported on the mainland or on Kent Peninsula.' (G. Abraham.)

3. SNOWY OWL

1942–43 was a poor year generally for snowy owls throughout the Arctic and Subarctic; nowhere were they reported abundant except at three posts on Victoria Island and they are said to have migrated eastward from Cambridge Bay in November. Most posts reported scarcity, including those in the Eastern Arctic where some increase had occurred.

4. SLEDGE DOGS

Investigation of disease among sledge dogs has been included in this Enquiry in order to find out if there is any connexion between 'crazy' disease in dogs and the periodic decimation of arctic foxes. So far (1935–42) there has been almost no evidence of 'crazy' disease, though details have been given about several epidemics of distemper similar to those which afflict the 'bush' posts farther south. Symptoms in 1942–43 were much the same as those reported in previous years and seemed characteristic of distemper or disorders due to starvation or food poisoning. (Details are on file in Oxford, but for the sake of brevity have been omitted from this report.)

1942–43, like the previous year, was singularly free from any kind of disease in sledge dogs north of the timber line. In Manitoba 'distemper' continued to kill off dogs and became more prevalent in Saskatchewan; also in Alberta, from which province (presumably) it spread into the Northwest Territories. Thus there always remains the danger of another epidemic sweeping the Arctic as it did in 1938–39. The only outbreaks noted in the Arctic and Subarctic are given below.

River Clyde. '20 pups under 6 months old were affected in February and all died. There was a gradual wasting away, they would not eat, got very thin, then paralysed in the hind quarters.' (J. G. Cormack.)

Fort George. 'In March 40 dogs died out of 60 affected. Young dogs were affected more than older ones: frothing at the mouth, paralysis of hind quarters, discharge from eyes and nostrils. Tape worms.' (R. M. Duncan.)

24. *Fort Providence and Hay River*. 'Some form of distemper was observed during late April, May and early June. In mild cases there was loss of appetite, discharge from eyes and nose. More severe cases suffered convulsions and frothing at the mouth. Most of the dogs were affected, quite a number died. Believed to have originated at Hay River.' (C. V. Teeple.)

Fort Providence. 'In April distemper affected 75% of the dogs, 40% mortality.' (D. McKinnon.)

Hay River. 'About 20 dogs were affected and all died. No symptoms before death.' (G. H. Parsons.)

5. SUMMARY

1. Sixty-nine replies were sent in with information about changes during 1942–43 in the numbers of lemmings (*Lemmus* and *Dicrostonyx*), arctic foxes (*Alopex lagopus*) and snowy owls (*Nyctea nyctea*) in the Canadian Arctic and Subarctic. Practically no information came from Northern Labrador.

2. Arctic foxes had crashed throughout the Eastern Arctic except in northernmost Baffin Island where moderate abundance was maintained. On the west coast of Hudson Bay where they had crashed the previous year there were signs that recovery was beginning. In the Western Arctic foxes were increasing or abundant and may have reached a peak.

3. 1941–42 had been a peak year for foxes in northern Quebec, southern and central Baffin Island, around the southern part of Hudson Bay and James Bay and on Southampton Island—in each area four years after the previous peak.

4. Lemmings were abundant only on the islands of the Western Arctic. They had crashed in central and southern Baffin Island, at Repulse Bay and on Southampton Island and had disappeared along with 'mice' around southern Hudson Bay and James Bay. In all these areas 1941–42 had been a peak year—culminating a four-year cycle—except in the case of Repulse Bay and Southampton Island where the last crash had been reported in 1936–37.

5. Lemmings were scarce for the second year in northern Quebec and northern Baffin Island and on the west coast of Hudson Bay. In the last area there were some reports of increase in 1942–43 and in northern Baffin Island observers expected recovery in 1943–44.

6. Snowy owls were scarce all through the Arctic and Subarctic except on Victoria Island where lemmings were still abundant.

7. There were only a few isolated epidemics of 'distemper' among the sledge dogs of the Arctic; but more extensive outbreaks were reported north and south of the Alberta boundary, in central Saskatchewan and Manitoba.

6. ACKNOWLEDGEMENTS

In this, the eighth report of the series, information on lemmings, Arctic foxes and snowy owls has been taken from 19 reports received through the Northwest Territories Administration, Ottawa, and 50 received through the Hudson's Bay Company, Winnipeg. Information about sledge dogs was obtained from these and many other reports received through the same channels.

We are very grateful to all those who have helped to keep this Enquiry going: to the men who answer the yearly questionnaires, to Mr R. A. Gibson, the Deputy Commissioner of the Northwest Territories, Ottawa, and Mr R. H. G. Bonnycastle and Dr L. Butler, Winnipeg, who were responsible for collecting and forwarding the replies, and to the Governor and Committee of the Hudson's Bay Company who have given us financial support.

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1. **Chitty, D. & Chitty, H. (1941).** 'Canadian Arctic Wild Life Enquiry, 1939–40.' J. Anim. Ecol. 10: 184–203. (Contains references to previous papers.)
2. **Chitty, D. & Nicholson, M. (1942).** 'Canadian Arctic Wild Life Enquiry, 1940–41.' J. Anim. Ecol. 11: 270–87.
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APPENDIX

Table 1. *Summary of observers' statements about Arctic fox, lemmings, 'mice', snowy owl and sledge dog for* 1942–43.

The following abbreviations are used: I. = increase, D. = decrease, N. = no change, s. = scarce, a. = abundant, × = neither.

Sledge dogs: o = disease reported absent. o* = slight disease or starvation reported, + = more serious disease.

Square brackets indicate observations that have been partly or entirely omitted from map or Table 2: (1) parts or all of some areas are not mapped if they are certainly outside the animal's range or cannot be located; (2) in groups 2 and 3 reports from inland posts are not mapped or included in Table 2; (3) reports on 'mice' and events at special times of the year are not included in the maps or Table 2.

Numbers in heavy type are the serial numbers of the replies to the government questionnaire. Unnumbered replies were received from the Hudson's Bay Company.

Table 1 (*continued*)

	Arctic fox	Lemmings	['Mice']	Snowy owl	Sledge dog
Group 1. Northern Labrador coast					
Cartwright, north to [Test Bay], south to Frenchman's Island. (R. M. Howell)	N. s.	—	I. a.	I. ×	o
Rigolet, south 50, north 75, west 35 miles. (G. Budgell)	I. ×	none	D. s.	N. ×	o
Northwest River [and inland 500 miles]. (R. G. Gillard)	D. s.	—	I. ×	D. ×	o
Group 2. Coast of Northern Quebec, south to Richmond Gulf [and inland]					
Georges River, north-west 30–40, west-south-west 50–80, south-east to north-east 70–100 miles. (J. A. Ford)	D. s.	D. ×	D. ×	D. s.	o*
September to October	—	—	[a.]	—	—
Along coast, *September to November*	[a.]	—	—	—	—
Fort Chimo to Leaf River and Whale River and inland 50 miles. (S. J. Stewart)	D.	D. s.	—	D. s.	o
Until April	[s.]	—	—	—	—
[Fort McKenzie, south 150, west 75, north 100 miles, east to Labrador.] (S. E. Dawe)	[D. s.]	[D. s.]	D. s.	[D. s.]	—
Payne Bay, north to Burgoyne Bay, south to Leaf River, inland 50 miles. (P. Dalrymple)	D. s.	D. s.	D. s.	D. s.	o
Sugluk, from Wakeham Bay to Sugluk West [and radius 150 miles inland]. (H. B. Figgures)	D. s.	D. s.	—	I. ×	o
Wolstenholme, south along coast to Kovik, then inland 20, south-east 30 miles. (L. Budgell)	D. s.	D. s.	D. s.	D. s.	o
Cape Smith; Island, and mainland from Kovik River to Kingwa River. (S. G. Ford)	D. s.	D. s.	—	D. s.	o
Povungnetuk, north to Mosquito Bay, south to Kogaluk Bay, inland to Payne Lake. (W. Davidson)	D. s.	D. s.	D. s.	D. s.	o
Port Harrison, north to Koklak River, south to Nastapoka River [inland to Long. 73°]. (R. Cruikshank)	D. s.	D. s.	D. s.	D. s.	o
Group 3. South parts of Hudson Bay, James Bay [and inland]					
Great Whale River, north to Richmond Gulf, south to Cape Jones [inland 100 miles]. (R. K. Muir)	D. s.	N. s.	N. ×	N. ×	o
Fort George, north to Cape Jones, south to Paint Hills, inland 50 miles. (R. M. Duncan)	D. s.	none	N. ×	I. s.	+
[Kanaapuscow to Fort George and north, east and south 50 miles radius.] (J. Berzink)	[D. s.]	—	N. ×	[I.]	—
[Nitchequon, north and north-east 50–75 sq. miles.] (T. A. Hambling)	[D. s.]	[D. s.]	—	[N. ×]	o
Factory River, to Eastmain and Fort George Rivers [inland 120 miles]. (A. E. Lillava)	D. s.	[N.]	N.	I.	o
Eastmain, Lat. 52–52·5° [inland to Long. 75°]. (R. C. Ross)	D. s.	—	D. s.	I. s.	o
Moose Factory and 40 miles radius	s.	—	N. s.	s.	—
Moosonee and 60 miles radius. (C. C. Foreman)	none	—	N. s.	—	o
Albany, 50 miles each side of Albany River [inland 100 miles]. (W. B. Anderson)	none	—	D. s.	D. s.	o
Attawapiskat, south to the Lawashi River, north to the Ekwan River [inland 150 miles]. Also Agamiski Island. (A. H. Michell)	D. s.	—	D. ×	D. ×	o
Weenusk, north 70, south 30, west [150] miles. (J. Mathieson)	D. s.	[D. s.]	D. s.	—†	o
Severn, west 50, east 10, up Severn River [150] miles. (F. H. Schoales)	N.	—	N.	—	o
York Factory and 50 miles radius. (H. F. Blank)	N.	none	D. s.	N.	o

† Conflicting reports: N. × and I. a.

Table 1 (*continued*)

		Arctic fox	Lemmings	['Mice']	Snowy owl	Sledge dog
	Group 4. West coast of Hudson Bay, north from Nelson River and inland					
	Churchill to Cape Churchill [north to Long Point], and inland 50 miles. (R. B. Urquhart)	D.	N.	N.	none	o*
16.	Churchill west 150, north 125 miles. (A. N. Anderson)	D. s.	D. ×	—	D. s.	o
12.	Churchill [to Northern Indian Lake] along Churchill River. (R. Stafford)...	D. s.	I. ×	—	N.	o
	Caribou, from mouth of North Knife River north to mouth of Big River, west to Nueltin Lake, south-east to Knife Lake, north-east to Knife River ...	D. s.	N. ×	N. ×	N. ×	o
	Eskimo Point and 50 miles radius. (A. Gavin) ...	D. s.	D. s.	D.	D. s.	o
	Late April, May		[I. a.]	—	[I. a.]	—
	Padlei, north and south 20 miles, east to west end of Maguse Lake, north-west to Yathkyed Lake. (H. Voisey)	I. ×	I. ×		I. ×	o
	Tavani; north to Rankin Inlet, then west to Kaminuriak Lake, then south to Maguse Lake, then north-east to Tavani. Also islands east of Tavani 20–30 miles. (J. A. Trafford)	D. s.	D. s.		N. ×	o
	Chesterfield Inlet, from Marble Island to Chesterfield and inland 70 miles. (For fox, north from Depot Island to 20 miles north of Whale Point: I; south and west of Chesterfield Inlet: D.) (A. R. Scott)	† D. × / I.	D. × / —	— / —	D. s. / -	o / —
29.	Chesterfield Inlet south to Mistake Bay, north to Wager Bay. (For fox, north of Inlet: I; south to Mistake Bay: D.) (L. E. Corey)	† D. s. / I.	I. a. / —	— / —	D. s. / —	o / —
31.	Baker Lake, and 150–200 miles radius. (J. H. Davis)	N. ×	I. a.	—	N. ×	o
(27).	Baker Lake and radius 120 miles. (A. Lunan) ...	N. ×	I. a.	—	I. ×	o
	Group 5. Southampton Island, Repulse Bay and Melville Peninsula					
35.	Repulse Bay, Pelly Bay and Lyons Inlet. (D. Drysdale)	N. ×	D. s.	—	D. s.	o
	Southampton Island.. (C. Russell)	D. s.	D. ×	—	D. ×	o
	Group 6. Southern Baffin Island					
	Lake Harbour from Robinson Sound and Frobisher Bay. (R. H. Kilgour)	D. ×	D. ×	—	D. ×	o
37.	Lake Harbour, west to Amadjuak, east to Gabriel Strait, Frobisher Bay and north [to Anderson Channel]. (D. P. McLauchlan)	D. ×	D. s.	—	D. s.	o
38.	Pangnirtung, to south coast of Cumberland Sound, and north shore of Home Bay; inland 70 miles. (W. E. Hastie)	D. ×	N. ×	—	D. ×	o
	Group 7. Northern Baffin Island, and north					
	River Clyde to Coutts Inlet and middle Home Bay. (J. G. Cormack)	D. ×	D. s.	—	D. s.	+
	Pond Inlet, Eclipse Sound, Navy Board Inlet, south to Coutts Inlet. (A. T. Swaffield)...	N. ×	N. ×	–	N. s.	o
	Spring	—	[I.]	–	—	—
39.	Pond Inlet; to Milne Inlet, south-east to north end of Home Bay. (H. A. McBeth)	N. ×	N. ×	-	D. s.	o
	Arctic Bay; from Cape Joy due south to Lat. 71°, thence circling round Fury and Hecla Straits to Bernier Bay and back to north end of Berlinguette Inlet, then along west coast of Admiralty Inlet to Cape Crauford. (J. Bell)	N. ×	D. ×	-	D. s.	o

† Shown as semi-circles in Fig. 1.

Table 1 (*continued*)

		Arctic fox	Lemmings	['Mice']	Snowy owl	Sledge dog
	Group 8. Boothia Peninsula and Islands west and north					
	Fort Ross, Boothia Peninsula, Somerset and Prince of Wales Islands. (W. A. Heslop)	I. a.	I. ×	I. ×	N. ×	o
	Cambridge Bay and 50 miles radius. (E. J. Gall)...	I. a.	I.	—	I.	o
	Up to November	—	[a.]	—	[a.]	—
30.	Cambridge Bay and 50 miles radius. (G. Abraham)	I. a.	I.	—	I.	o
	Up to November	—	[a.]	—	[a.]	—
36.	Richardson Island and north-east and west 100 miles. (O. Andreason)	I. a.	N. s.	—	N. ×	o
(34)	Read Island; Lady Franklin Point, west along coast to Williams Point, overland to Prince Albert Sound. (W. F. Joss)	I. a.	I. a.	—	I. a.	o
	Holman Island, from Investigator Island in Prince Albert Sound to Minto Inlet and Deans Dundas Bay. (H. W. Chitty)	I. a.	I. ×	—	N. ×	o
	Until January	[s.]	—	—	—	—
	Group 9. Pelly Bay, west to east of Coppermine River and inland to Back River					
	Bathurst Inlet and 300 miles radius. (M. L. Manning)	I.	I.	—	I.	o
	Group 10. Dubawnt Lake, west to Fort Rae and Fort Resolution					
	Fond du Lac and north. (L. A. Martin)	D. s.	—	N. ×	—	o
	Rocher River, east 100 and south [100] miles; (for arctic fox: east of Snowdrift). (R. Jardine) ...	I. a.	none	I.	N. s.	o*
	Snowdrift, north-east to Back River, east to Artillery Lake, south to Nanacho Lake. (S. R. Nunn)	I. a.	I. ×	I. a.	N. ×	o*
17.	Fort Reliance; Ptarmigan and Clinton Colden Lakes. (A. J. Knox)	I. a.	N.	s.(white)— × (brown)	N. s.	—
	After Xmas	[D.]	—	—	—	—
20.	Fort Reliance; north of Clinton Colden and Aylmer Lakes. (H. M. Silver)	I. a.	N.	s. (white)— × (brown)	N. s.	o*
	Around Thelon River, *during January*	[D.]	—	—	—	—
2.	Fort Reliance, north of west end of Aylmer Lake to Icy River near Muskox Lake. (G. Magrum) ...	I. a.	D. ×	—	N. ×	o
	Fort Rae, south-east 80 to Yellowknife River, east 150 to end of Snare Lake, north 150 to Hardisty Lake [north-west 150 to Lake la Martre, north-north-west 180 miles to Lac Grandin]. (J. E. J. Wilson)	D. a.	N. ×	I. a.	N. ×	o
	Yellowknife district. (A. Reid)	I. a.	rare	D. ×	I.	o
26.	Yellowknife; Gordon Lake to Mackay Lake and 50 miles north. (C. Watt)	I. ×	I. ×	—	none	o
	Group 11. Coppermine River to Alaska					
	Coppermine, south from Coronation Gulf to Great Bear Lake. (L. A. Learmouth)	I. a.	D. ×	—	D. ×	o
40.	Coppermine, west 50 miles on Rae River, then north to Stapylton Bay, east to Krusenstern, south to mouth of Rae River. (L. F. Semmler)	I. a.	D. ×	—	D. ×	o
32.	Liverpool Bay, west to Cape Dalhousie, east to Baillie Island. (S. Mason)	I. a.	N. s.	—	N. s.	o
	Tuktuk, from mouth of east branch of Mackenzie River, north to Cape Dalhousie, east to Kugalook, east of Huskie Lakes, west to west shore Richards Island. (J. E. Sidgwick)	I. a.	—	I. a.	N. ×	o
	Arctic Red River and radius of 50 miles. (L. Roy)	—	—	N. ×	—	o
4.	Arctic Red River and radius 50 miles north and east [west 70 miles, south 120 miles]. (A. C. Gillespie)	rare	rare	—	N. ×	o
	Aklavik and 100 miles radius	D. ×	—	N.	—	—
5.	Mackenzie River Delta. (L. Weston)	I. ×	N. ×	—	N. ×	o*

Table 2. *State of the Arctic fox, lemming and snowy owl populations in* 1942–43. *Number of observers reporting relative abundance compared with* 1941–42.

	Eastern Arctic									Western Arctic					
Group no. ...	1	2	3	4	5	6	7	Total	%	8	9	10	11	Total	%
Arctic fox:															
Increase	1	.	.	2	.	.	.	3	**8**	6	1	7	5	19	**86**
Decrease	1	8	6	7	1	3	1	27	**69**	.	.	2	1	3	**14**
No change	1	.	2	2	1	.	3	9	**23**	.	.	.	.	.	.
Total	3	8	8	11	2	3	4	39	**100**	6	1	9	6	22	**100**
Lemming:															
Increase	.	.	.	5	.	.	.	5	**17**	5	1	2	.	8	**47**
Decrease	.	8	.	4	2	2	2	18	**62**	.	.	1	2	3	**18**
No change	.	.	1	2	.	1	2	6	**21**	1	.	3	2	6	**35**
Total	.	8	1	11	2	3	4	29	**100**	6	1	6	4	17	**100**
Snowy owl:															
Increase	1	1	3	2	.	.	.	7	**19**	3	1	1	.	5	**25**
Decrease	1	7	2	4	2	3	3	22	**59**	.	.	.	2	2	**10**
No change	1	.	2	4	.	.	1	8	**22**	3	.	6	4	13	**65**
Total	3	8	7	10	2	3	4	37	**100**	6	1	7	6	20	**100**

COMPARATIVE STUDIES OF THE HABITAT REQUIREMENTS OF TSETSE FLY SPECIES

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1. OBJECT OF THE INVESTIGATION

For some years now investigators have studied the changes in numbers of tsetse flies by means of regular catches conducted over fixed routes, and the changes in mean weight and its constitution in samples of flies. For the most part these investigations have failed to afford any explanation of why different species are more or less segregated in distinct habitats, a phenomenon inexplicable by *a priori* reasoning, and one which therefore offers hope of unpredictable discoveries, and perhaps ultimately of practical advantage. A notable exception is the work of Nash (1936, 1940) in Nigeria, who has observed that *Glossina tachinoides* Westwood is somewhat more susceptible than is *G. submorsitans* Newstead to very high temperatures, and he has been able to relate the differences in late dry-season habits of concentration of these two species to the difference in viability.

It seemed that in East Africa it might be profitable to compare the two closely related species *G. morsitans* Westwood and *G. swynnertoni* Austen, in order to obtain some clue to the reason for their vegetational or climatic preferences. It should be recalled that *G. morsitans* is generally associated in East Africa with what is known as the *miombo* formation, dominated by associations of *Isoberlinia-Brachystegia* broad-leaved deciduous woodland; while *G. swynnertoni* seems to avoid this type and is found in the thornbush dominated by *Acacia* and *Commiphora* communities. There are, however, many known exceptions in the distribution of *G. morsitans* even in Tanganyika.

It was considered that the best way to explore this subject was to introduce each of the two species into the habitat of the other, and to throw in also *G. palpalis* Robineau-Desvoidy, normally a waterside species, as likely to afford a more striking indication of how a tsetse community might be expected to appear when introduced into an environment to which it was presumably quite unsuited.

Some preliminary field observations have now been made, and have been supported by a small amount of laboratory work. So far it has been possible only to introduce *G. morsitans* (twice) and *G. palpalis* (once) into the habitat of *G. swynnertoni* (living with *G. pallidipes* Austen); the converse experiment of putting *G. swynnertoni* and *G. palpalis* into the habitat of *G. morsitans* has not yet been attempted, but it is hoped to do this in the future.

Observations of interest bearing on tsetse population studies, and on the accumulation of fat, have been made in the course of this investigation, but discussion of them will be reserved to a more appropriate occasion.

Flies which have lost weight rapidly, or which have not recently fed, are deficient in water, fat and residual dry weight, especially the first two. Under favourable conditions, also, fat and residual dry weight increase with age, at least for some weeks. The weight of fat is therefore an indication of the well-being of the fly community at any one time of year. However, the weight of flies at emergence varies with the seasons, smaller individuals emerging at the hotter times of year; and in any batch of flies emerging on the same day there is always considerable variation in weight, which is related to variation in size. To correct weight for size, I have made use of a wing-vein measurement (see below). This method is not satisfactory for individual flies, but works fairly well for batches.

2. OUTLINE OF THE FIELD EXPERIMENTS

The introductions were made in a more or less isolated block of country (about 8 miles by 6) near Shinyanga in Tanganyika, heavily infested by *G. swynnertoni* in the north, and less heavily in the south which had been unburnt for some years. *G. pallidipes* was common in the more thicketed south and scarcer in the north.

Pupae of *G. morsitans* were obtained from the Kondoa district of the Central Province. In the first experiment they were exposed in a Stevenson screen for the last 10 days of October 1943 in the south part of the block, in a concentration area of *G. swynnertoni*. During these 10 days it was estimated that about 300 of each sex emerged and flew away. In the second experiment, larger numbers were exposed in two sites 5 miles apart for a fortnight in early May 1944, during which time it was estimated that about 1232 of each sex emerged in the south of the area, and about 422 of each sex in the north. In addition, pupae of *G. palpalis* (from Entebbe, Uganda) were exposed during the same fortnight in the south of the area, close to a pool by a seasonal stream which formed a habitat of *G. pallidipes*. It was estimated that about 287 of each sex emerged. Finally, more *G. palpalis* pupae were exposed in open thornbush in the north for a fortnight in late May–early June, when it was estimated that about 350 of each sex emerged.

A map and description by H. Harrison (1936) of the country used (block 9) will be found in this

Journal, vol. 5, p. 271. The southern release sites were in square C2, and the northern one was near the intersection of H2 and 3, G2 and 3.

The flies were recovered mostly on regular routes, some followed daily except on Sundays and some at longer intervals; in the second series routes followed daily for 17 weeks were arranged so as to form squarely angular spirals with the release sites at their centres.

When a *G. morsitans* non-teneral* (fed) male was recovered, it was inserted in a small tube ($2 \times \frac{1}{4}$ in.), ordinarily together with the next non-teneral male *G. swynnertoni* to be captured, and the tube was then numbered and sealed with wax, the flies in due course dying of asphyxia. Teneral (unfed) males, and males of *G. palpalis*, were treated similarly, but not accompanied by *G. swynnertoni* controls.

After arrival at the laboratory, the flies were removed from the tubes and weighed at about 2.30–3.00 p.m. on a torsion balance, and subsequently their water, fat and residual weights were taken. This was done by heating to constant weight in a steam oven, then alternately putting them in chloroform and heating, until again a constant weight was obtained. Weights were read to 0·1 mg., but flies reweighed and found to be within 0·1 mg. of the previous weight were taken as having reached the constant weight sought.

3. THE FIRST FIELD EXPERIMENT

This was carried out near the end of the dry season, and except for two or three isolated storms the rains had not broken when the first generation of flies had disappeared. In the tables which follow, the water percentage is of fatless weight, and the fat percentage is of waterless weight. Weights are in mg.

From Table 1 it is concluded that in the late dry season *morsitans* in the habitat of *swynnertoni* is slightly lighter in all respects than *swynnertoni* magnified to the same size, but that both are lighter in all respects than the control *morsitans* at the corresponding season 8 years before in their own habitat (Kakoma, Tabora district: Jackson, 1937).

In Table 1 the last *morsitans* male to be captured was between 29 and 39 days old. There was then an interval of 29 days, after which (the rains having broken) several *morsitans* were caught, including a male and a female teneral fly, and these and later recaptures (from 28 December to 15 February) are believed to represent part of a second generation. In Table 2 they are compared with their *swynnertoni* controls, and with *morsitans* controls from 1935.

In this case we do not know by what factor to multiply the weights of *swynnertoni*, but it is evident from Table 2 that the *morsitans* are considerably heavier in their own habitat, besides having more water and fat proportionately, than in the habitat of *swynnertoni*.

* 'Teneral' is the word used for flies with unhardened chitin. The chitin does not become hard until after the first meal of blood, which is normally taken about 3 days after emergence.

4. THE SECOND FIELD EXPERIMENT

The second release of *morsitans* in north and south, and the southern release of *palpalis*, were made from pupae exposed from 3 to 17 May, when the dry season was beginning. Recaptures of the first generation flies continued for over 12 weeks after removal of the pupae, and some of them overlapped with the first flies of the second generation (of *morsitans*), from which however they were readily distinguished by their tattered wings.

Table 1

Species	Water	Fat	Residue	Water %	Fat %	No.
Teneral males under 24 hr. old (laboratory)						
morsitans	13·90	1·28	4·77	74·36	21·04	28
swynnertoni	13·56	1·13	4·47	75·15	19·89	27
Teneral males at large						
morsitans	11·00	0·62	4·51	70·83	11·83	12
swynnertoni	9·73	0·50	4·21	69·61	9·61	28
Non-teneral males at large						
morsitans	17·00	2·23	6·98	70·88	23·18	94
swynnertoni	16·46	2·32	6·99	70·16	24·26	90
Non-teneral males divided by 0·96						
swynnertoni	17·15	2·42	7·28	—	—	90
Controls from *morsitans* habitat at same season in 1935						
morsitans	17·31	2·67	7·42	70·00	25·85	120

The penultimate line is obtained by dividing the previous line of *swynnertoni* by 0·96, because it appears from the teneral laboratory controls that this species is about 96% of the weight of *morsitans* at this season.

Table 2

Species	Water	Fat	Residue	Water %	Fat %	No.
Teneral males at large						
morsitans	11·2	0·4	4·2	73·0	9·0	1
Non-teneral males at large						
morsitans	17·30	2·46	7·24	70·6	23·2	10
swynnertoni	15·97	2·12	6·87	69·9	22·5	10
Controls from *morsitans* habitat at same season in 1935						
morsitans	22·24	3·01	8·76	71·7	24·7	35

In Table 3 the teneral male *morsitans* controls are from two batches taken before and after exposure, the *palpalis* from a single batch taken after exposure of the pupae. There are no controls for the *swynnertoni*, as pupae could not be obtained at this season. All the non-teneral flies except the *palpalis* are from the spiral fly rounds only; the teneral *swynnertoni* and

all the *palpalis* are from other catches besides the spiral rounds. It will be recalled that *swynnertoni* was more numerous in the north of the area, which was therefore probably more suited to it, than in the south. Herds of big game were more numerous in the north.

In Table 3 *morsitans* appears to have more water in the south of the area, but more fat in the north. *Swynnertoni* has more fat and residue in the north, but not less water. In both north and south, *morsitans* is somewhat heavier in all respects than *swynnertoni*, but lighter in all respects, and especially in fat, than in its own habitat. *Palpalis* in the south is rather

Table 3

Species	Water	Fat	Residue	Water %	Fat %	No.
Teneral males under 24 hr. old (laboratory)						
morsitans	15·74	1·27	5·54	73·92	17·36	39
palpalis	14·08	1·67	5·44	73·00	22·90	20
Teneral males at large in north						
morsitans	12·58	0·75	5·10	71·00	12·59	5
swynnertoni	11·62	0·68	4·74	70·94	12·35	17
palpalis	17·30	2·00	6·00	74·00	25·00	1
Teneral males at large in south						
morsitans	13·67	0·70	5·39	71·59	11·07	42
swynnertoni	13·00	0·74	5·03	72·10	12·60	10
palpalis	14·51	1·27	5·56	72·50	18·07	14
Non-teneral males at large in north						
morsitans	18·49	2·57	8·27	69·09	23·00	56
swynnertoni	16·93	2·40	7·56	68·95	22·53	56
palpalis	11·70	0·40	6·00	66·00	6·00	1
Non-teneral males at large in south						
morsitans	19·37	2·41	8·34	69·80	21·19	143
swynnertoni	16·94	2·12	7·46	69·35	21·10	121
palpalis	17·75	2·28	7·52	70·28	22·67	54
Controls from *morsitans* habitat at same season in 1935						
morsitans	20·52	3·03	9·10	69·33	23·59	61
Controls from *morsitans* habitat at same season in 1944						
morsitans	20·64	3·21	8·86	69·91	24·22	77

The control non-teneral males came (1935) from Kakoma, Tabora district, in May and June, and (1944) from Kahama district on 4 June.

light in weight, but has high proportionate fat and water contents. In the north only one non-teneral individual was recovered, and that was desiccated and starving. The rather light weight of the *palpalis* in the south is partly accounted for by the subtraction of six recently fed individuals for blood examination. Of these five had recognizable blood meals, of which all were reptilian and one was certainly terrapin, as the corpuscles and Haemogregarines corresponded to those found in the blood of terrapins examined. *Palpalis* was able to feed on a terrapin in the laboratory.

Again, in the absence of teneral *swynnertoni* controls, it was not immediately possible to correct the *swynnertoni* weights for the smaller size of that species, and all that could be noted at this stage was that the residual weight was proportionately higher than in *morsitans* or in *palpalis*.

5. CORRECTION FOR DIFFERENCE IN SIZE BETWEEN SPECIES

Pupae of *swynnertoni* became available from June, and altogether five batches of teneral male *morsitans*, three of *swynnertoni* and four of *palpalis* were examined and analysed in the months April to August 1944. After preliminary work, it was decided to use as a criterion of size the length of a vein in the wing, and the vein (middle part of the 4th longitudinal) corresponding to the cutting blade of the hatchet cell was chosen. This vein was measured in all the individual flies dealt with, both teneral controls and flies recovered from the field.

Briefly, it was found that the correlation between vein length and weight was very poor in *palpalis*, whether in batches or as individuals. For individual *morsitans* or *swynnertoni* the correlation coefficient of weight with vein was between +0·4 and +0·5, but

Table 4

Species	Water	Fat	Residue	Water %	Fat %	No.
Non-teneral males from north						
morsitans	18·49	2·57	8·27	69·09	23·00	56
swynnertoni	18·53	2·62	8·28	68·95	22·53	56
Non-teneral males from south						
morsitans	19·37	2·41	8·34	69·80	21·19	143
swynnertoni	19·70	2·47	8·68	69·35	21·10	121

much better for batches of flies. Further, it was found that in the range of weight in which these two species overlapped *swynnertoni* had a vein averaging about 0·063 mm. less than in *morsitans* of the same weight. When this amount was subtracted from all the *morsitans* veins, the correlation coefficient for individuals of both species taken together was +0·48 (201 flies), and for the eight batches taken together it was +0·97, a value good enough for the working of regression coefficients. The mean vein length being known for all batches of flies recovered from the field, it was then possible to calculate the probable mean weights of these field flies when they were under 24 hr. from emergence, and so to find the probable relation at that stage between the mean weights of the non-teneral *morsitans* and *swynnertoni* examined. (It should be mentioned that there was no suggestion from the data that the relation betweeen vein length and weight was anything but linear, though it had been supposed that the weight would probably be related to the square or cube of the wing vein.)

Using this method to correct for the smaller size of *swynnertoni* in Table 3, I obtained the result set out in Table 4.

The correction to produce Table 4 was made separately in the north and in the south, because it was found that the *swynnertoni* sample from the north had a significantly longer mean vein. This table indicates that, when allowance has been made for difference in size, *swynnertoni* is slightly heavier in all respects, but has lower mean water and fat percentages, than *morsitans* in the same habitat. *Swynnertoni* is still much lighter in all respects than is *morsitans* in its own home.

6. LOSS OF WEIGHT IN THE LABORATORY

Being disappointed in finding no more striking difference between the native and the introduced species in the habitat of *swynnertoni*, and at a loss to account for the great difference between both species in the habitat of *swynnertoni* on the one hand and *morsitans* in its own habitat on the other, I attempted to compare the rates of loss of weight under laboratory conditions. This work was done in late July and early August 1944. The temperature remained approximately constant in an inner room at a mean of 25·3°C. Relative humidity was kept constant at 50% by means of caustic potash solution as described by Buxton & Mellanby (1934). Teneral males under 24 hr. old were weighed individually between 9.30 and 10.30 a.m., and five of each of the three species, *morsitans*, *swynnertoni* and *palpalis*, were then exposed for approximately 24 hr. to the conditions described. The experiment was done twelve times in all, involving 60 flies of each species, and the same number of controls was killed at once for analysis, so that altogether 360 flies were analysed. Three *palpalis* and one *morsitans* died and were replaced.

The data were dealt with as follows. Regression coefficients (adding to unity) were worked from the controls of each species, for respectively water, fat, and residue, on wet weight. From these and from the mean values of the controls it was then possible to calculate the probable weights of water, fat, and residue together composing the known initial weight of each fly; and as the final values of these quantities were determined directly, it was possible to say with reasonable accuracy how much of each component any particular fly had probably lost.

The only significant difference was that *G. palpalis*, as expected, lost more water and more total weight than either *morsitans* or *swynnertoni*. The most interesting fact that emerged, however, was that *swynnertoni* lost slightly more weight than did *morsitans*, instead of less, as both its smaller size and its presumed adaptation to a supposedly severer environment might have led one to expect. If a correction is made (as before) to all mean weights and losses of *swynnertoni*, the losses actually work out significantly higher than those of *morsitans*, which is another way of saying that *swynnertoni* loses proportionately more of its weight under the same conditions.

Further, the rule seems to hold good for individuals within any one species. The experiment was divided into first and second halves, and correlation coefficients were worked for each half and each species, between weight lost and initial weight. The coefficients obtained were −0·21 and +0·16 for *morsitans*, +0·19 and +0·33 for *swynnertoni*, and +0·14 and +0·21 for *palpalis*. The mean value of z is +0·1383 and its standard error is ±0·07192. As the expectation is that z would be positive if anything, the positive 0·1 point, +0·1183, may be taken as the borderline of significance, so that the correlation is just significant. As, however, with a correlation of this magnitude, over 95% of the variation in loss is unaccounted for by variation in initial weight, the correlation is clearly negligible, and it may be stated

Table 5

	Water	Fat	Residue	Wet weight
	Controls			
morsitans	15·862	1·620	5·338	22·820
swynnertoni	13·594	1·144	4·506	19·244
palpalis	15·725	1·790	5·472	22·987
	Experimental flies			
morsitans	—	—	—	22·090
swynnertoni	—	—	—	19·866
palpalis	—	—	—	23·068
	Estimated losses			
morsitans	2·696	0·297	0·170	3·165
swynnertoni	2·749	0·329	0·186	3·263
palpalis	3·157	0·346	0·234	3·738

Table 6

Species	Mean initial weight	Mean loss	No.
pallidipes	28·34	3·63	9
morsitans	21·20	3·76	7
swynnertoni	18·88	4·12	5

that for all practical purposes individuals lose weight regardless of what they have to lose.

This result was extremely surprising, and it was felt desirable to compare species showing a greater initial difference in mean weight. A few *G. pallidipes* pupae became available in August, and seven teneral females under 24 hr. old were subjected to the same conditions as above, together with seven female *morsitans* and five female *swynnertoni* (Table 6).

Only three male *pallidipes* were tested, and one of these (which may have been injured in handling) lost 6·2 mg., but the other two lost about the same as three male *morsitans* and three male *swynnertoni*.

It therefore appears that within the *morsitans* group individuals and species lose weight practically regardless of what they start with, and it follows that, among teneral flies at least, smaller species under the same conditions must be at a disadvantage in the field. There is evidence that this is so among individuals, because the mean vein length of the first

generation of *morsitans* was significantly smaller in teneral than in non-teneral males at large, indicating a natural weeding out of smaller and therefore less viable individuals. In *palpalis* this was not observed, but the mean vein of teneral males at large was longer than that of teneral males emerging in the laboratory.

7. THE SECOND GENERATION FROM THE SECOND FIELD EXPERIMENT

One object of the second experiment was to discover whether the numerous *swynnertoni* in the north of the area would interfere with the breeding of the fewer *morsitans* allowed to emerge there, as appeared probable from the work of my colleague, Mr F. L. Vanderplank.* A positive result was obtained, with a probability less than 0·01. Practically no second generation appeared in the north, but in the south a considerable second generation was in full swing when the work was closed. The analyses of these flies and their controls are given in Table 7.

Table 7

Species	Water	Fat	Residue	Water %	Fat %	No.
Teneral males at large						
morsitans	12·08	0·85	4·75	71·33	14·17	6
Non-teneral males at large						
morsitans	17·39	2·73	7·57	69·76	25·80	41
swynnertoni	16·92	2·52	7·24	69·49	24·78	41
Non-teneral males corrected for difference in size						
swynnertoni	17·28	2·58	7·39	—	—	41
Controls from *morsitans* habitat at same season in 1935						
morsitans	19·97	2·65	8·67	69·78	22·60	55

For controls for the teneral males, take those in Table 5.

The correction to the *swynnertoni* weights in this case is very small, because the wing veins indicate that there was very little mean difference at emergence between individuals of the two species composing the samples. This suggests that *morsitans* is being born smaller in the *swynnertoni* habitat than in its own home; though here we must be careful, because the samples of teneral laboratory flies already given show that in the later dry season there is apparently less difference in weight between the two species than in the early dry season: *morsitans* appears to put on more weight than *swynnertoni* in the cold weather after the rains.

No second generation of *palpalis* has been observed, though the pool where the release took place did not dry up until after the second generation was due, and about half the first generation females recovered from the field and maintained by Mr Vanderplank in the laboratory produced normal larvae, and, in due course, imagines.

* Mr Vanderplank found that in the laboratory mating between the two species was practically random; that females inseminated by the alternate species were mostly barren; and that those which were not, produced only a few hybrid offspring, most of which were sterile.

8. DISCUSSION

The observations so far made have not told us why *morsitans* and *swynnertoni* live in different vegetational types, but they have shown that samples of both species taken from the habitat of *swynnertoni* are lighter in weight than samples of *morsitans* from its own habitat. Such samples of insects as these, to which the catchers act as bait, cannot be regarded as random samples of the whole community of either species; but if they may be taken as an indication, it does seem that *morsitans* put into the habitat of *swynnertoni* is physiologically inferior to *morsitans* in its own home. Further, even though the samples are not representative of the whole community, one would expect an occasional fly to be caught with, for example, something approaching the maximal weight of fat; whereas not only is the mean weight of fat in the exiled *morsitans* less than in *morsitans* in their proper habitat, but (which is not brought out in the tables) the three fattest exiles had 5·4, 5·4 and 5·8 mg. of fat, much less than a considerable proportion of the *morsitans* samples from their own home (6–7 mg.).

This deficiency cannot be directly from lack of food, because the thornbush type of Shinyanga carries a much more numerous population of big game than the *miombo* country of Tabora and Kahama from which the control groups of *morsitans* were drawn; and the standard climate of these places is not less severe than that of Shinyanga. We are therefore left to suppose that the ecoclimate of the thorn is more severe than that of the *miombo*, because of the less complete vegetational cover.

The laboratory experiments show that teneral *swynnertoni* are not more, but less resistant than *morsitans*, and if the same applies to non-teneral flies it seems that *swynnertoni* must either seek out more sheltered resting sites, or take more frequent meals, in order to survive at all. But their physiological condition resembles that of the exiled rather than of the native *morsitans*, which implies that their choice of resting sites does not entirely counterbalance the unfavourable ecoclimate; and in fact a very common resting site of *swynnertoni* is on the under side of the branches of small *Commiphora* trees 2–4 m. above the ground, where they are practically at the normal air temperature of the standard climate.

I therefore make the provisional suggestion that *swynnertoni* (living with a relatively heavy game population) is in some way specially adapted to take more frequent meals than *morsitans*. There is slight evidence that this is so, because the *swynnertoni* samples contain a higher proportion of solid residue, and a

lower proportion of fat and water, than *morsitans* in the same environment, and part of this solid residue is assumed to be faecal matter from the previous meal. Also, in a previous experiment (August 1941), of 14 wild male *swynnertoni* released and recaptured at their original weights to the nearest milligram, no fewer than eight were recovered within 2 or 3 days, whereas *morsitans* in similar experiments has nearly always taken longer to return to approximately the original weight.

Presumably *morsitans* in the habitat of *swynnertoni* has equal opportunities to take frequent meals; but perhaps it is less adept at finding its food under those conditions, or its physiology is not suited to such frequent feeding, because it does not seem able to produce the reserve of fat which is natural to it, and in spite of its apparently greater resistance to desiccation, it is in no better conditon than *swynnertoni*.

The reason for the absence of a second generation of *palpalis* is a mystery. However, it seems that something may go wrong in the pupal stage, because the males recovered seemed to be in fairly good condition, the females duly became pregnant, and a good proportion of those recovered from the field produced viable larvae in the laboratory.

9. SUMMARY

1. *Glossina morsitans* and *G. palpalis* have been introduced into the habitat of *G. swynnertoni* and *G. pallidipes*.

2. The mean weight of *morsitans* recaptured was not greatly different from that of *swynnertoni* after making allowance for the difference in size, but both were considerably lighter than *morsitans* in its own environment.

3. *Morsitans* in the environment of *swynnertoni* can produce a second generation, but apparently *palpalis* cannot.

4. The numerical size of the second generation appears to depend on the amount of interference with the breeding by *swynnertoni*, as suggested by the work of my colleague Mr F. L. Vanderplank.

5. *Palpalis* in the habitat of *swynnertoni* (but on a seasonal stream) fed mainly on reptiles, including terrapin.

6. *Pallidipes*, *morsitans*, *swynnertoni* and *palpalis* teneral flies in the laboratory seem to lose weight almost without regard to their initial weight. *Palpalis* loses water and total weight more rapidly than the others under the same conditions. In the *morsitans* group, smaller species and smaller individuals among teneral (unfed) flies lose practically the same amount of weight as do larger species and individuals, and therefore lose more proportionately. It follows that, other things being equal, smaller individuals and smaller species are at a disadvantage.

7. It is conjectured that *swynnertoni* counteracts this disadvantage by adapting itself to taking more frequent meals, which it is able to do because it is accustomed to live among a heavy population of Ungulate animals.

8. There is a suggestion that in the habitat of *swynnertoni* the individuals of the second generation of *morsitans* are smaller in size than they would be at home. This suggestion however has not yet been proved.

9. Much further work on these lines is needed before any firm conclusions can be drawn.

10. ACKNOWLEDGEMENTS

I am very grateful to Mr J. D. Gillet, of the Uganda Medical Department, for arranging the regular purchase and dispatch of pupae of *Glossina palpalis* to Shinyanga.

This investigation has fitted in very well with the concurrent hybridization studies of Mr F. L. Vanderplank, whose flyboys provided many of my recaptures, and who maintained the recaptured females in the laboratory to observe the numbers and nature of their offspring. He also took wet weights of flies during two periods when I was away.

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BIOGRAPHICAL NOTICE

DANIEL N. KASHKAROV

The death of Professor Kashkarov, in November 1941, was received with regret by ecologists in this country, but the slowness of wartime communication with Russian scientists has prevented until recently the preparation of an adequate notice of his life and research. Now, through the courtesy of Dr N. I. Kalabukhov in Moscow, some further information has come to hand, which, together with published work, allows an appreciation to be made of Kashkarov's wide experience and the lines of his achievement. He was a great ecologist, certainly the greatest animal ecologist who has yet appeared in Russia: I say Russia, because his early training took place under the well-known Russian zoologist Michael A. Menzbir, before the first World War. It was, however, after the Revolution that he had the expanding opportunities for research and travel that have resulted in his extensive series of publications on ecological subjects.

Most of his original investigation was done while he lectured and studied in the Middle Asiatic State University at Tashkent. Perhaps it was a good thing that a man with his capacity for field work was not immediately to get engulfed in the administrative preoccupations of the Soviet capital. There were fascinating opportunities for ecological expeditions in Uzbekistan, Turkmenya and Kazakstan. The animal communities and especially the mammal populations, both wild and domestic, of the huge desert and desert marginal grazing land attracted him especially, and were described in several papers, including one with Kurbatov in English in *Ecology* (1930), 11: 35–60, on the vertebrate fauna of the Central Kara Kum Desert, which shows a lucid and interesting mind, and a high capacity for field observation. This survey was done by a carefully mixed team of botanist, soil scientist, vertebrate zoologist, invertebrate zoologist and a farming expert, together with some younger naturalists, and was a model of ecological reconnaissance. The remarks that 'all the animals of the desert, including man and his domestic animals, constitute one system in equilibrium' and that 'the adaptation to desert condition is rather in behavior than in structure, because the chief factors in deserts are climatic, and adaptations to climate are more in behavior than in structure' denote an outlook on ecology that is modern and dynamic.

During this middle period of his life, Kashkarov was evidently incubating and beginning to discuss various ideas about the structure of communities and ecosystems, and essayed several contributions to the philosophy of the subject that are, unfortunately, not yet translated for the general reader here and in America. Some of them are listed by Carpenter in his review of Soviet ecology (*J. Anim. Ecol.* (1939), 8: 354–86). His field study, with Lein, of the Turkestan yellow ground squirrel (*Cynomys fulvus*), which hibernates and aestivates for about eight months of every year, revealed a degree of successful adaptation by this species to peculiar habitat factors that may well have seemed almost topical in a human community faced with staggering difficulties of agricultural ecology, though he would hardly have applied to man the biological implication in the life of this curious rodent, that the most successful species is one that stays asleep under shelter for the longest time without starving! Kashkarov drew upon this first-hand experience of rodents, domestic animals (such as the karakul sheep), and birds, for a manual, prepared jointly with V. V. Stanchinskii, on the biology of vertebrates, published in 1928, and reprinted in 1935 and 1939 as a standard textbook of the zoology of vertebrates for the use of Soviet university students.

From this work in connection with the programme of reconstruction of agriculture in Central Asia, he went on to develop more general concepts on ecology. These found expression in a book called *Environment and community* (*principles of synecology*). This 244-page Russian book was later amplified and much more fully illustrated in *Principles of the ecology of animals* (Moscow and Leningrad, 1938, 601 pp.; in Russian). The latter book was briefly reviewed by Dr B. P. Uvarov in the *Journal of Animal Ecology* (1939), 8: 171–2. It is greatly to be desired that this book should be translated in full, since it evidently represents a full treatment of current Soviet ideas on animal ecology by a man who was by training not at all unsympathetic to the progress of scientific ideas outside the U.S.S.R. (An earlier small book on the life of the desert (1936) had apparently been translated into French; but this would be dealing with less general matters.)

Kashkarov, it always seemed to me, had an excellent background of general European and American ecological ideas that were derived from wide reading, and from his tour of European biological stations in 1911, and a visit to America in 1923. This no doubt enabled him to understand the futility of isolating part of what is a world science, even within the bounds of a very large and varied empire. This balance of outlook in him led him incidentally to translate a little text-book of my own (*The ecology of animals*, London, 1933) into Russian, where it was published in 1934: a fortunate privilege for me, as it led to exchange of publications and other research information with Soviet ecologists, which I value highly. His membership of various learned societies abroad (including the British Ecological Society) also showed the international basis of his scientific interests.

In 1934 Kashkarov became Professor of Vertebrate Zoology and Ecology in the University of Leningrad, where he exercised a considerable influence upon the subject and also helped to direct editorial work. He had already, in 1931, started the *Journal of Ecology and Biocenology*, of which, however, only one volume appeared; but continued it with a useful journal (little known outside the U.S.S.R.) devoted to the ecology of all groups of animals, *Problems of Ecology and Biocenology*, of which at least seven parts have appeared.

When the War threatened Leningrad, Kashkarov refused to leave, and stayed on during the gruelling days of the blockade, giving talks to the Red Army soldiers on methods of camp life, the illusory race-theories of the Nazis, and other topics. When the University finally was compelled to move its staff away to Ruibinsk, he went

with them, but died of heart failure during the journey. He was then in his 64th year.

Here was evidently a man of considerable ecological talents, whom one would very much have liked to meet, who strove to make reasonable generalizations from his wide field experience and reading, and whose interests were not confined either by personal taste or official compulsion to purely economic problems. When his work is generally available in English, we shall be able to gain from it an impression of the trends in Soviet ecological thought during the last twenty years. We shall not find ourselves in agreement with all these ideas, but we should see how eagerly and on what an enormous scale the Soviet authorities have encouraged the growth of ecological research on a broad basis of primary surveys and research on basic principles. One may hope that Kashkarov's work, which really contains a successful fusion of ideas derived from Soviet Russia and from the scientific world outside Russia, is an omen of the frank exchange of information and personal discussions between the Soviet ecologists and ourselves that one hopes will come.

In conclusion, it may be mentioned that Kashkarov was an excellent painter, and that his scenes of Central Asia and other parts of Russia were exhibited in the Leningrad Scientists' House.

CHARLES ELTON

REVIEWS

LAND ECOLOGY

Edward H. Graham (1944). *Natural principles of land use.* 274 pp., 8 text-figures and 32 photo plates. Oxford University Press (London, New York and Toronto). Price $ 3·50.

Dr Graham is Chief of the Biology Division in the United States Soil Conservation Service. Soil erosion has been a big problem in the United States in recent years, and has been tackled by Federal and State governments with great energy. From the obvious need to replace vegetative cover on eroded areas or to control plant succession or deterioration on watersheds, it was a short step to attempt management also of the animal life both in its ecological relations to the success of soil and vegetation growth, and as a source of agricultural income or amenity on the recovering farm lands. Hitherto there has been a good deal written in periodicals upon all these aspects of the main problems, and a great deal upon the physical, chemical and geological qualities of soils themselves. Dr Graham's book is the first to give a thoroughly balanced survey of the different elements in this complicated picture. He tries, and with considerable success, to give parallel accounts of the scientific basis of plant and animal ecology, and of the human problems of agriculture, forestry, fisheries, water supply and other uses of the land and its natural products. The brilliant bibliography at the end, one of the best ecological literature selections that I have seen, convinces the reader of the author's scientific accomplishment, while the examples given in the text show an obviously first-hand acquaintance with land ecology and management in the field. In this he is following the fine tradition of the United States Federal wild life services, by combining scholarship with travel and knowledge of animals and plants in their natural habitats.

The main idea running through this book is a dynamic one: that good land management means the balancing of different demands, the harmonizing of various components that are in unstable equilibrium, or have lost all equilibrium through previous specialization or neglect; and planning things so that immediate gain is not cancelled out by some more distant loss or disaster. This idea is rammed home by a series of very good photographs showing the results of good and bad land treatments, and especially photographs taken before and after modern types of control have been carried out. Thus we see a prairie graveyard standing now three feet above surrounding country that had not been fenced against agricultural misuse; barren gullies rehabilitated by the planting of suitable shrubs and herbs, or dammed up to make productive freshwater habitats that can grow fish and muskrats; the growth of cactus where pasture is overgrazed; the revetment and planting of bare stream banks to form luxuriant new habitats; contour ploughing; and the planting of special cover and food-plant strips for wild animal and bird life. The most attractive series of pictures is of the reconstructed history of New England, with primitive mixed forest, cleared and turned into pioneer farm land, abandoned for better land or town life and then reverting by ecological succession into pine forest, which when cut-over became a hardwood forest once more.

There is a clear account of some of the ecological principles known about animal communities and population changes. Throughout the treatment is original, the style fresh and the arrangement of matter (considering the complexity of the subjects that have to be dealt with) logical. Animal ecologists will be especially interested to find their subject constantly referred to in discussions of the control of land. Usually land managers have thought animal life one of the last things to worry about—a luxury, or if not, at any rate a natural result of providing vegetation on a physiographic background, that requires no direct management or forethought. Graham gives many examples of the importance of animals as destructive agents, vectors of disease, helpers in forest regeneration, sources of food, or of pleasure. He sounds a warning note on the introduction of exotic forms.

Altogether, this book gives a very sound impression of the growing points in ecology that bear upon land use, without making the mistake of over-estimating the chances of applying such knowledge successfully in the present elementary state of our subject, which still has more technical terms than sound concepts, more chaotic facts than co-ordinated studies, and yet is subject to a terrific pressure of demand for the solution of economic problems. I think Dr Graham knows just how we stand in the subject, and has written a book that will interest all kinds of people who find training in land ecology necessary or interesting.

CHARLES ELTON

ORNITHOLOGY

Joseph J. Hickey (1943). *A guide to bird watching.* 263 pp. Some text-figures. Oxford University Press (London, New York and Toronto).

The tidal wave of research and observation upon wild life in the United States that was sweeping into publication before the War, has no doubt made a good many American ecologists feel the need for guidance about methods and principles by which to assess all these detailed results and follow them up further in the field. Although Mr Hickey writes from the Department of Wildlife Management of the University of Wisconsin, this book is not about the use and abuse of bird life, but simply about birds as such. It deals with the same general field as the two best books previously published in this country, by Nicholson (1931) and Fisher (1940), concentrating mainly upon methods of studying migration (including marking methods), taking censuses, relation of birds to habitats and to ecological succession, and various other opportunities open to the bird watcher. A useful and original appendix deals with bird tracks, with illustrations of some of these by Charles Urner, a distinguished amateur ornithologist whose field work in this subject is recorded here for the first time. Another appendix summarizes useful data about the population densities of breeding birds. Another lists in the true ecological American style all the things you could do in a field study, including 'how does the weight of each egg vary from day to day' and 'at what age do the young first react with fear to moving cardboard outlines of hawks and owls'—all very stimulating and intelligent. The literature on birds is discussed, but there is no detailed reference list to examples mentioned throughout the text of this book, nor unfortunately to the list of breeding bird densities. There are many interesting examples and attractive anecdotes which give reality to the advice on methods of research, and these are in a setting of sound ecological information and ideas.

CHARLES ELTON

Margaret Morse Nice (1943). *Studies in the life history of the song sparrow.* II. Trans. Linn. Soc. New York, Vol. 6, 328 pp.; frontispiece, 6 text-figures.

This volume completes the intensive study by Mrs Nice of the song sparrow, *Melospiza melodia*, by means of colour ringing and watching a population for seven years. The first part was published in 1937 and dealt with population statistics. The present volume deals with life history and behaviour, and the material drawn from the song sparrow has been amplified by an exhaustive study of the literature about other passerines. The result is a general consideration of passerine behaviour, in which data, otherwise scattered, have been drawn together and brought into a general picture of the progress of such work. Naturally this volume is not of such direct interest to the ecologist as the previous one, but in many ways it forms an important addition to his library.

Chapters 2–5 give a very detailed study of the development of young song sparrows with particular attention to the time and mode of appearance of different aspects of their behaviour. Much of this is based on observing hand-reared birds, but these observations are satisfactorily extended by data from the field. Chapter 7 deals with social behaviour in the non-breeding season and discusses the type of social dominance found against the background of types seen in other species.

Chapter 8 contains an interesting analysis of the times of awakening and roosting in relation to light intensity and other factors, showing that light is the most important. Song is discussed in Chapters 9–11, territory in Chapters 12–13, reproduction in Chapters 14–20 and finally some aspects of behaviour in Chapters 21–22. There is a full bibliography and good indexes.

Throughout the work the original observations are the most valuable, though their very bulk has made them difficult to arrange without a multiplicity of divisions and subdivisions, and this is at times bewildering. The extensions from the literature on other passerines are extremely useful for reference (the reviewer knows no other work in which so many sources are brought together), but the discussions are not comparably increased in value.

There could be no better example of the amount that can be achieved by painstaking and prolonged observation. At the same time this book constitutes a warning that problems of behaviour will never be solved by this method alone. Some link between natural historian and physiologist becomes increasingly desirable, and experiments designed by the latter in the light of the former's results hold out the greatest hope of any significant advance in resolving fundamental problems.

H. N. SOUTHERN

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3*s.* 6*d.* per annum post free (in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. Chitty, C. Elton, B. M. Hobby, Barrington Moore, F. T. K. Pentelow and U. Wykes.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and brackish

Atkins, W. R. G. (1944). 'Plant nutrients in the sea.' Nature, Lond. 154: 489–90.

The annual turnover in phosphorus in the English Channel is about 1 ton per sq. km. Comparatively little of the naturally occurring phosphate sinks permanently out of circulation into the depths of the sea.

Ritchie, J. (1944). 'Plant nutrients in the sea.' Nature, Lond. 154: 832.

The rate of application of phosphorus on arable land is greater than would be required in the sea. Fertilizers are almost immediately converted into phytoplankton so that dissipation is checked.

Gordon, I. (1944). 'An Amphipod, *Orchestia bottae*, new to Britain.' Proc. Linn. Soc. 155: 70.

This species, the most terrestrial of the genus, was found under stones above high water mark on the banks of the Thames near Isleworth Ferry, Richmond. It is widely distributed in Europe, but this is its first appearance in this country and it may have been introduced with soil to Kew or in sand used for the building up of the embankment.

(*b*) Fresh water

Underdown, H. C. B. (1944). 'Birds of the riverside: V. The Dipper.' Salm. Trout Mag. Lond. 112: 215–17.

A popular account of the distribution and habits (particularly feeding and nesting) of *Cinclus c. gularis*.

Lloyd, B. (1944). 'Dragonflies of Pembrokeshire.' Entomologist, 77: 113–18.

Records of 18 species with some ecological details of habitat.

Laurie, W. H. (1944). 'Nymphs in Border Waters: observations on the hatch in rapid rivers.' Salm. Trout Mag. Lond. 112: 222–30.

Careful observations, in natural waters and in aquaria, on the process of transformation of Ephemeroptera (*Ecdyonurus* and *Baëtis*) from the aquatic nymph to the aerial sub-imago.

Warwick, T. (1944). 'Inheritance of the keel in *Potamopyrgus Jenkinsi* (Smith).' Nature, Lond. 154: 798–9.

This snail has a smooth or keeled shell depending on the presence of a certain alga during its early life.

Scourfield, D. J. (1944). 'The nannoplankton of bomb-crater pools in Epping Forest.' Essex Nat. 27: 231–41.

130 species were found: from 1–48 species per crater. There was no special difference between the nannoplankton of craters and other small bodies of water.

(*c*) Land

Rothschild, M. (1944). 'Pelage change of the stoat, *Mustela erminea* L.' Nature, Lond. 154: 180–1.

A change from brown to white pelage did not occur solely because of a reduction in the duration of light, though this may have a complementary effect to that of a lowered temperature.

Massee, A. M. (1944). 'Notes on some interesting insects observed in 1943.' Rep. E. Malling Res. Sta. 31 (1943): 58–65.

Notes and observations on 22 species of insects and other animals, including the first record of the occurrence in Great Britain of the mite *Pediculopsis graminum*.

Petherbridge, F. R. & Stapley, J. H. (1944). 'Two important wheat pests.' J. Minist. Agric. 51: 320–4.

Includes notes on life history and food plants of the wheat bulb fly (*Leptohylemyia coarctata*) and the wheat shoot beetle (*Helophorus nubilis*).

Crombie, A. C. (1944). 'On the measurement and modification of the olfactory responses of blowflies.' J. Exp. Biol. 20: 159–66.

Froggat suggested that the native blowflies of Australia became conditioned to the smell of sheep wool when, during droughts, the adults laid their eggs on sheep carcasses. They were consequently attracted to the wool of living sheep also and, when mature, used it for oviposition, causing great economic damage. The present experiments show that blowflies, though normally repelled by menthol, can be habituated to this odour in the larval stage and the habit is then preserved after metamorphosis. The populations of habituated flies were not, however, homogeneous in their responses.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Gregor, J. W. (1944). 'The ecotype.' Biol. Rev. 19: 20–30.

The status of the ecotype has been affected by the variable definition of the word ecospecies. This term was introduced by Turesson in 1922 to draw attention to the species as an ecological unit as apart from its genotypic construction. In his subsequent redefinitions of the term it approximates more and more to the usual definition of a species, i.e. a group of actually or potentially interbreeding natural populations which are reproductively

isolated from other such groups. The only reason for the retention of the term 'ecospecies' is that it indicates a species which has been taxonomically delimited by experiment. Populations which can interbreed, but in which the capacity for gene exchange is limited, e.g. chromosome races, are then in different coenospecies although they would be in a single ecospecies.

The ecotype is defined as 'the product arising as a result of the genotypic response of an ecospecies to a particular habitat'. The question arises 'What, if any, is the difference between the ecotype and the subspecies'? Various definitions of subspecies are given. These frequently coincide closely with the conception of the ecotype; but where the morphological characters are stressed as the ultimate criterion of the subspecific boundary, the group may include two or more physiologically differentiated ecotypes. There is no reason to suppose that these *ecotypic* subspecies are biologically different from or less valuable than the orthodox *morphological* subspecies of the taxonomist. It is suggested that the term 'ecotypic' or 'ecoclinal' subspecies be retained for those groups whose limitations cannot be determined by inspection but require experimental technique.

L[egge], C. M. (1944). 'A new method of preparing and storing mammal skins....' Yearb. N.W. Nat. Union, 1941–3: 25.

Summary, with good line illustrations, of method of preparing flat mammal skins, developed by C. Elton (1938).

Smart, J. (1944). 'The British Simuliidae, with keys to the species in the adult, pupal and larval stages.' Sci. Publ. Freshw. Ass. Brit. Emp. No. 9: 1–57. Price to non-members 2*s.* 6*d.* (The Director, Freshwater Biological Association, Wray Castle, Ambleside, Westmorland.)

Authoritative summary with illustrated keys, notes on general ecology and distribution, and special distribution and habitats in the Lake District. Selected bibliography.

Collin, J. E. (1944). 'The British species of Anthomyzidae (Diptera).' Ent. Mon. Mag. 80: 265–72.

Keys to genera *Diadelops*, *Paranthomyza*, *Anagnota*, and *Anthomyza*.

Collin, J. E. (1944). 'The British species of Psilidae (Diptera).' Ent. Mon. Mag. 80: 214–24.

Keys to the genera *Chyliza*, *Loxocera*, and *Psila*. This family includes the carrot fly.

Hicken, N. E. (1944). 'Larvae of the British Trichoptera. 20.' Proc. Ent. Soc. Lond. A, 19: 9–12.

Illustrated description of *Neuronia ruficrus*.

Dougherty, E. C. (1944). 'The lungworms (Nematoda: Pseudaliidae) of the Odontoceti. Part I.' Parasitology, 36: 80–94.

The writer regards the lungworms of porpoises as a distinct family, Pseudaliidae of the superfamily Metastrongyloidea, which includes some closely related lungworms of terrestrial mammals. This separation is supported by the unique structure of the female reproductive organs in this family and the reduction of the bursa in the male which has also a typical pattern of fusion of the rays. These structures may be of considerable phylogenetic significance since variation therein might restrict mating and so act as an isolating mechanism.

3. PARASITES

Milne, A. (1944). 'The ecology of the sheep tick, *Ixodes ricinus* L. Distribution of the tick in relation to geology, soil and vegetation in northern England.' Parasitology, 35: 186–96.

Ticks infest about 800 sq. miles of the four northern counties. Their occurrence is strictly limited to rough grazings, which are the product of poor soil or poor drainage due to underlying glacial deposits of clay. The thicker the vegetation layer the greater the density of ticks.

Baylis, H. A. (1944). 'Observations on the nematode *Mermis nigrescens* and related species.' Parasitology, 36: 122–32.

Casual records collected at the British Museum for 22 years show that this worm is widely distributed in Great Britain. Of 91 dated records 16 were in May, 56 in June and 19 in July. This is the season when the females migrate from soil to herbage for oviposition. Since many records came from suburban gardens where

the usual hosts, grasshoppers, would be uncommon, eggs of *Mermis* were fed to other animals. Positive results were obtained with earwigs, which sometimes acquired lethal infections and which were also found to be commonly infested under natural conditions. There is an indication that in *light* infections the worms are all females, while if the host carried 13 or more larvae they were all males.

Arthur, D. R. (**1944**). '*Aphidius granarius*, Marsh., in relation to its control of *Myzus kaltenbachi*, Schout.' Bull. Ent. Res. 35: 257–70.

The rate of reproduction is high, the sex ratio of the progeny of mated females is about 12·9 : 10, but unfertilized females produced only males. Adults live 21–27 days and fly readily when the temperature is 25°–30° C., the wind velocity below 7 miles per hour and the relative humidity about 70%. The factors limiting the effectiveness of the parasite, e.g. susceptibility to thermal change, oviposition failure, supernumerary larvae and meteorological conditions restricting flight, are discussed.

Massee, A. M. (**1944**). 'Further notes on the woolly aphid parasite (*Aphelinus mali* Hald.).' Rep. E. Malling Res. Sta. 31 (1943): 65–7.

A brief account of attempts to establish the parasite in Kent from 1924–38. Its reappearance in vast numbers in the summer and autumn of 1943 is discussed.

Blair, K. G. (**1944**). 'Some galls of *Lipara lucens* Mg. (Dipt., Chloropidae) from Norfolk.' Ent. Mon. Mag. 80: 189–90.

Galls of this fly were collected in two different fens near King's Lynn, one of them scarcely touched by man, in the latter habitat the flies were much more heavily parasitized and the variety of casual inhabitants and other parasites was also very much greater.

4. FOOD AND FOOD HABITS

Roebuck, A., Baker, F. T. & White, J. H. (**1944**). 'The grazing of winter cereals by the wood-mouse (*Apodemus sylvaticus*).' J. Anim. Ecol. 13: 105–9.

In Nottinghamshire, Lincolnshire, Derbyshire, Leicestershire and Rutland winter cereals near woods are extensively attacked by *Apodemus sylvaticus*. Unlike rabbit attack, the plants are cut smoothly to within about ½ in. of the ground along a well defined 'feeding front' which may advance 5 yd. per night, equivalent to 0·3 acre. Severe attacks necessitate ploughing, others lower the yield and quality of grain, and delay harvesting. Prebaiting and poison baiting with dry crushed oats plus 4% zinc phosphide are effective, but must be repeated fortnightly because of immigration.

Sawyer, F. E. (**1944**). 'Feeding trout with natural food: a new use for fly boards.' Salm. Trout Mag. Lond. No. 112: 239–43.

The author found, by autopsy, that for the first fortnight of their feeding life, trout fry feed almost exclusively on small chironomid larvae, and thereafter on ephemerid nymphs (principally *Baëtis* spp.). He accordingly constructed a stew designed to encourage the production of these food organisms and found that the stock of ephemerid nymphs could be artificially increased by the use of 'fly boards'.

Grensted, L. W. (**1944**). 'Insects attracted to young laurel shoots.' Ent. Mon. Mag. 80: 296.

Visitors to extra-floral nectaries included an astonishing number of insects, mostly Diptera and small Hymenoptera, with a few Coleoptera (all Coccinellidae). Names are given.

Evans, A. C. (**1944**). 'Observations on the biology and physiology of wireworms of the genus *Agriotes* Esch.' Ann. Appl. Biol. 31: 235–50.

A study of the feeding activity and moulting frequency showed that small wireworms grow more rapidly and moult more frequently than large ones. Thus a method for the analysis of wireworm populations has been found. The type of crop grown after breaking up old pasture directly affects the damage done to the following cereal crop. This is chiefly due to the effect of the food on the rate of growth of the wireworms.

Thorpe, W. H., Crombie, A. C., Hill, R. & Darrah, J. H. (**1945**). 'The food finding of wireworms (*Agriotes* spp.).' Nature, Lond. 155: 46–7.

Wireworms aggregate on entering a part of the soil which contains plant substances above a threshold concentration. Some of these substances cause aggregation only, some only release a biting response, others, such as sugars, do both.

Melville, R. (1944). '*Ailanthus*, source of a peculiar London honey.' Nature, Lond. 154: 640–1.

44% of the pollen present in some unpleasant-tasting honey from a Kensington apiary consisted of the tree of heaven *Ailanthus altissima*, pollen of sweet chestnut (*Castanea sativa*) also being present. Both these trees have flowers with unpleasant smell. Other notes on flavours of honey derived from various plants are given.

Elton, C. (1945). 'Honey from *Ailanthus*.' Nature, Lond. 155: 81.

Honey bees in Oxford visiting male flowers of *Ailanthus altissima* in large numbers.

Farmiloe, C. (1945). 'Sources of London honey.' Nature, Lond. 155: 80–1.

The presence of pollens in honey is not a quantitative guide to the sources of the nectar. The strong smell found by Melville, R. in some London honey is probably due to privet (*Ligustrum vulgare*). Chief sources of London honey are lime (*Tilia europaea*), privet, and—since the war—*Epilobium angustifolium* growing on bombed sites. Lime produces little pollen, and other species of pollen may be well represented in honey mainly derived from this tree.

Scott, H. (1944). 'Black ants (*Acanthomyops niger* L.) (Hym., Formicidae) collecting rosemary seeds and dead Coleoptera.' Ent. Mon. Mag. 80: 207–8.

Seeds of rosemary are evidently a favourite article with harvesting ants; perhaps the aromatic nature of the plant makes it attractive.

Lloyd, R. W. (1944). 'Dolichopodid fly associated with bark-beetles.' Ent. Mon. Mag. 80: 180.

The Dipteron *Medeterus nitidus* and other species of the same genus have been bred several times from galleries of bark beetles and the larvae have been observed attacking larvae and pupae of the beetles. *M. nitidus* is here associated with *Scolytus intricatus*.

Carpenter, G. D. H. (1944). 'Natural selection in the six-spot burnet moth.' Nature, Lond. 154: 239–40.

Great tits attack cocoons on a wire fence or hawthorn hedge or object on which they can perch. Cocoons on tall waving grass stems were not so damaged.

Goodey, T. (1944). 'A note on the feeding of the nematode, *Anguillulina macrura*.' J. Helminth. 21: 17–19.

A. pratensis and *A. obtusa* feed and reproduce wholly within the root tissues of grasses. *A. macrura*, however, was never found to enter a root completely, though specimens were found in which the œsophageal region was inserted. This species appears at present to be an intermittent parasite, living freely in the soil, but penetrating the root cortex with its anterior end for feeding.

Pantin, C. F. A. & A. M. P. (1944). 'The stimulus to feeding in *Anemonia sulcata*.' J. Exp. Biol. 20: 6–13.

Mechanical, chemical or electrical stimulation of tentacles can start feeding reactions if sufficiently prolonged. Adaptation to mechanical stimulation is rapid; thus inert objects rarely produce a feeding reaction, though they may cause a rejection reaction which occurs to brief stimulation. Chemical stimuli set up a more prolonged excitation. Sensitivity is greatest to animal foods and seems to be due to protein derivatives. The fats tried and most carbohydrates are without effect.

5. POPULATION STUDIES

Matheson, C. (1944). 'The domestic cat as a factor in urban ecology.' J. Anim. Ecol. 13: 130–3.

The introduction of the domestic cat into Britain dates back at least to the Roman period, as shown by excavations in the Roman city at Silchester, Hampshire. A questionnaire to school children in Cardiff and Newport, Wales, showed cats as percentage of people ranging from 5·5% in the more modern houses to 15·2% in the older quarters, with an average of 10·4%. Figures from other large cities gave a ratio of stray cats to people of between 2 to 3%. A minimum of about 13% is estimated to be the ratio of cats to human population in towns.

Southern, H. N. (1944). 'A transect census of pigeons.' J. Anim. Ecol. 13: 134–9.

In order to test a method of finding the density of a species within its range, counts of wood pigeons (*Columba palumbus*) and stock doves (*C. oenas*) were made from a train during two journeys between Berkshire and Devonshire. The stock dove is more abundant except at the western end of the transect. The total count of nearly 400 for both species represents a density of about 1·5 birds per mile, including built up areas and railway cuttings.

Hardisty, M. W. (1944). 'The life history and growth of the brook lamprey (*Lampetra planeri*).' J. Anim. Ecol. 13: 110–22.

Spawning grounds which are frequently at the same place from year to year, appear related to shade, depth of water, swiftness of current and barriers. Spawning temperature lies between 10 and 11° C. Frequency curves indicate a larval period of 3½–4 years and total life of 4 or 5 years. Growth in length is greatest during the first 1½ years, then declines, but increases again in the final stages. The weight-length relation does not follow the cube law. There appears to be a reduction in length at sexual maturity.

Beirne, B. P. (1944). 'The abundance of wasps (Hym., Vespidae).' Ent. Mon. Mag. 80: 272.

Further data are given in support of the view that spring rainfall is one of the main factors regulating wasp abundance.

Morley, B. D. Wragge (1944). 'A study of the ant fauna of a garden, 1934–42.' J. Anim. Ecol. 13: 123–7.

The ants' nests in a sandy soil with a south exposure in a 2½ acre garden at Bournemouth were mapped, and the changes are shown in three maps covering respectively 1934–7, 1938–40 and 1940–2. There were six species, and the success of the various species, in terms of area foraged over and dominated, fluctuated greatly. *Acanthomyops mixtus* abandoned its underground habits when in a mixed colony with *A. fuliginosus*. Large polycolic colonies seemed more successful than single nests.

Oliver, F. W. (1944). 'A mass catch of cabbage whites by sundews.' Proc. R. Ent. Soc. Lond. (A), 19: 5.

It is estimated that six million cabbage whites were caught in a patch of sundews on an island of about two acres in Sutton Broad, Norfolk, on 4 Aug. 1911.

Edelsten, H. M. (1944). 'Contribution to the life-history of *Oria musculosa* Hübn. (Lep. Noctuidae).' Entomologist, 77: 145–8.

In the Salisbury district this moth, formerly considered a rarity, has much increased in numbers owing to cessation of crop rotation during the war period and the placing of stacks along the edges of fields which may carry a cereal crop the following year. If these practices continue, the species may become a serious pest.

Allen, F. (1944). 'Notes on a plague of antler moth at Greenfield.' Yearb. N.W. Nat. Union, 1941–3: 25–6.

Brief observations on outbreak of *Charaeas graminis* on a square mile of grassland, that was accompanied by migration and very high density of caterpillars, and attacks by birds.

Barnes, H. F. & Weil, J. W. (1944). 'Studies of fluctuations in insect populations. XI. The interrelationship of the wheat blossom midges and their host plant.' Ann. Appl. Biol. 31: 231–4.

The interrelationship of the wheat blossom midges and the wheat is so close that from the date of midge emergence the forwardness of the crop can be foretold and from the percentage grain attack by the larvae a first estimate of the crop yield can be made.

Miles, H. W. (1945). 'Wireworms and war-time farming.' J. Minist. Agric. 51: 462–7.

Contains figures of wireworm populations obtained in the national survey.

Common, A. F. (1944). 'A "plague of ladybirds" in Essex.' Entomologist, 77: 190.

Millions of 7-spot ladybirds (*Coccinella septempunctata*) settled along a seven mile front from Shoeburyness to Leigh-on-Sea, 30 July 1944.

Crombie, A. C. (1944). 'On intraspecific and interspecific competition in larvae of graminivorous insects.' J. Exp. Biol. 20: 135–51.

In females of *Rhizopertha* and *Sitotroga* the rate of oviposition is not related to the amount of food available. The larvae frequently indulge in multiple infestation of wheat grains, but the limiting factor in the ensuing struggle for existence is space; the number of larvae of the same age which survive on the same grain is less than that which the food present there could support. Where the two species are in competition the average ratio of survival is 1·3 R : S, where R and S are the original numbers of larvae of each species. This ratio only applies when the larvae enter the grains at the same time and at the same instar. Otherwise competition favours the first comers. Overcrowding encourages the survival of *Sitotroga* with retarded rates of development. These are able to survive in competition with normal larvae of the same species. This is possibly because larvae of approximately the same instar are less tolerant of each other than those of widely different instars.

Thomas, I. & Heal, Gwen M. (1944). 'Chafer damage to grassland in north Wales in 1942–1943 by *Phyllopertha horticola* L. and *Hoplia philanthus* Fuess. I. Notes on population, life history and morphology.' Ann. Appl. Biol. 31: 124–31.

P. horticola was largely confined to wooded river valleys, while *H. philanthus* was dominant in very sandy fields almost at sea level in the Portmadoc district. Soil sampling in November–December showed that practically all the *horticola* larvae were in the top 6 in. of soil. Selective sampling in damaged areas of fields, i.e. the areas badly scratched up by birds, and undamaged areas in the same fields revealed much higher populations (up to 1,850,000 per acre) in those areas visited by birds than in the undamaged areas. But undamaged areas of fields showed populations up to 600,000 per acre. Populations up to 2,750,000 per acre are recorded.

Broadhead, E. & Hobby, B. M. (1944). 'Studies on a species of *Liposcelis* (Corrodentia, Liposcelidae) occurring in stored products in Britain. Part II.' Ent. Mon. Mag. 80: 163–73.

The 'book-louse' *Liposcelis granicola* has four nymphal instars. The average duration of nymphal life at 25° C. and 76% R.H. varied from 15·1 days (on yeast) to 30·7 days (on a synthetic food). The average number of eggs laid per female in the first 50 days of adult life ranged from 5·8 (on a synthetic food) to 117·1 (on yeast). The average length of adult life was shortest (175 days) on food (yeast) promoting a large egg production (212 eggs) and longest (268 days) on food (flour) resulting in poor egg production (39 eggs).

Hughes, T. E. (1944). 'The respiration of *Tyroglyphus farinae*.' J. Exp. Biol. 20: 1–5.

These mites infest grain and flour. If exposed to pure CO_2 or atmospheric oxygen for 72 hours, the mites are killed, though they can survive such treatment for shorter periods. Experiments in which cultures living (*a*) in grain and (*b*) in flour were exposed to very low oxygen concentrations showed a more rapid response (inactivity, and finally death) in the grain cultures. This is because the atmosphere in flour is slow to come into equilibrium with the outside atmosphere.

Barnes, H. F. & Weil, J. W. (1944). 'Slugs in gardens: their numbers, activities and distribution. Part I.' J. Anim. Ecol. 13: 140–75.

About 100,000 slugs were collected in 1941–3 in certain gardens at Harpenden, Hertfordshire. The unit sample was the slugs picked up on a favourable night, without baiting or searching, during a 30 minute walk with a flashlight. The removal of the slugs collected did not appreciably affect the numbers in the population. Of the nine species collected, *Arion hortensis*, *Agriolimax reticulatus* and *Milax gracilis*, were the most abundant, showing yearly totals of roughly 10,000–11,000, 9000 and 5000–9000 respectively. Three other species, *Arion subfuscus*, *Milax sowerbyi* and *Arion ater*, showed about 1000–4000, while the three remaining species were much less common. A key is given for identifying 15 out of the 20 species recorded in the British Isles. The abundance of slugs is so great that the average for 351 half-hour periods during 1942 and 1943 was nearly 200 per period. Large numbers have been found at all times of the year when weather is favourable. Each species has its own rhythm in numbers active, and these pulsations occur annually with remarkable regularity. The seasons in which peak numbers occur are not the same for each species.

Barnes, H. F. (1944). 'Discussion on slugs. I. Introduction. Seasonal activity of slugs.' Ann. Appl. Biol. 31: 160–3.

The reliability of a method of sampling slug populations in gardens by collecting all those seen in half-an-hour after dark is established. The seasonal trends in numbers active of five species are briefly sketched.

Thomas, D. C. (1944). '[Discussion on slugs.] II. Field sampling for slugs.' Ann. Appl. Biol. 31: 163–4.

The use of metaldehyde-bran baits in (1) estimating the populations in fields as well as a method of converting the relative figures so obtained into absolute ones, (2) investigating slug damage and (3) the estimation of the efficiency of slug poisons on a field scale.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Jackson, R. A. (1944). 'Further notes on the spread of *Pararge aegeria* in Hampshire.' Entomologist, 77: 158–9.

For some years the speckled wood butterfly has been increasing in numbers in the Bishop's Waltham district.

Jackson, R. A. (1944). '*Hyloicus pinastri* spreading eastwards?' Entomologist, 77: 171.

Record of the pine hawk moth at Bishop's Waltham, Hampshire. Its original home was Dorset: in 1940 it had reached Brockenhurst in the New Forest, and in 1943 it was taken near Winchester. The latest occurrence is a further 7 miles east.

Fraser, F. C. (1944). 'Remarkable distance covered by nymphs of *Pyrrhosoma nymphula* (Sulz.) (Odon., Coenagriidae).' Ent. Mon. Mag. 80: 192.

Empty dragonfly nymphal exuviae were found on trees 7 ft. above ground and up to 30 ft. from the edge of the pond. The trees formed a narrow belt round the pond and as no exuviae were found on other suitable resting-places it is suggested that vast numbers must have walked on to the open common, where they would become an easy prey for birds and ants.

Butler, C. G., Jeffree, E. P. & Kalmus, H. (1944). 'The behaviour of a population of honey bees on an artificial and on a natural crop.' J. Exp. Biol. 20: 65–73.

112 dishes of sugar syrup were set at 20 yd. intervals in a meadow. Individual bees returned repeatedly to the same dish for one or more days. An alternative dish was visited rarely unless the original supply ran out, when the radius of search was extended. Dishes in shade were rarely visited. If different concentrations of syrup were offered simultaneously, the higher concentrations quickly became the most popular. The time taken in feeding from dishes was about 1 min. as against 20–60 min. on a flower head of *Echinops*. Marked bees visiting an isolated patch of this thistle returned constantly for up to 16 days and few strayed 18 yd. away to another patch.

Bently, E. W. (1944). 'The biology and behaviour of *Ptinus tectus* Boie (Coleoptera, Ptinidae), a pest of stored products.' J. Exp. Biol. 20: 152–8.

Adults were introduced into a humidity gradient from a moist environment. During the first week locomotary activity varied directly with the humidity, with the result that the animals accumulated in the drier region. But in desiccated animals the responses are reversed and they collect in the wetter region. Reactions to humidity differences are greatest at R.H. of below 70% or over 90%. Amputation experiments suggested two kinds of humidity receptors: those responsible for normal reaction being at the distal end of the antennae and those for the 'reversed' reaction being either on the basal joint or not on the antennae at all.

Lees, A. D. (1944). 'On the behaviour of wireworms of the genus *Agriotes* Esch. (Coleoptera, Elateridae). I. Reactions to humidity.' J. Exp. Biol. 20: 43–53.

Wireworms introduced into an alternative humidity chamber tend to congregate in the humidity nearest to 100% R.H. The scatter is less when saturation deficiency is used as a measure of humidity, suggesting that the reaction is initiated by evaporation. Humidities close to saturation, such as prevail in soil, are those over which reactions are most sensitive. The larvae are more active in dry than in moist air and if the wireworm crosses a steep gradient from moist to dry air there is a powerful recoil. These two types of reaction alone seem responsible for the final distribution.

Lees, A. D. (1944). 'On the behaviour of wireworms of the genus *Agriotes* Esch. (Coleoptera, Elateridae). II. Reactions to moisture.' J. Exp. Biol. 20: 54–60.

Alternative chambers were used containing sand differentially moistened. In order to eliminate gravity responses the chambers were rotated in different experiments, but no traces of such a response were found. The wireworms introduced migrated rapidly from dry to wet sand. This response depends on the fact that burrowing activity varies inversely as the moisture content. *Feeding* activity also seems much greater at low than at high moistures. This may explain why wireworms only do notable damage to crops when the saturation is less than 25%.

7. REPORTS OF ORGANIZATIONS

Christ's Hospital, West Horsham, Natural History Society: Thirty-Seventh Annual Report for the year 1943 [1944]. Horsham. 38 pp.

Records of insects, birds, density of soil organisms, fungi and plant succession in West Sussex. The rare migrant, Queen of Spain Fritillary, was taken.

L[egge], C. M. (1944). 'Summary of and notes on the Report made to the Nature Reserves Investigation Committee by the Sub-Committee for South Lancashire (S. of the Ribble) and Cheshire.' Yearb. N.W. Nat. Union, 1941–3: 19–22.

General reasons, with no biological details, for reserving 15 separate areas, including Ainsdale Sand-dunes, Rostherne Mere, various woods, marshes, pools, salt-marsh, and lowland peat-mosses.

Anon. (1944). 'Report on the Coward Nature Reserves.' Yearb. N.W. Nat. Union, 1941–3: 22–3.

General notes only, on three reserves. One was partly threatened by airport development. One of the others presents management problems in controlling woodland succession on to the peat-moss, and in vegetation changes following fire.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1944

Income

	£ s. d.	£ s. d.
Subscriptions received, including arrears, and *less* Payments in advance:		
Members taking *Journal of Ecology* only	270 0 0	
Members taking *Journal of Animal Ecology* only ...	175 11 5	
Members taking both Journals	148 5 0	
Associates	1 10 0	
		595 6 5
Interest on Investments	62 5 3	
Interest on Deposit Account	1 15 11	
		64 1 2
Profit on Redemption 5% Conversion Loan Stock ...		1 10 0
Grant from Royal Society		150 0 0
Journal of Ecology. Sales less Cost		241 6 4
Index to *Journal of Ecology*, vols. I–XX, Sales ...	9 10 0	
Less Expenses	1 8 7	
		8 1 5
		£1,060 5 4
Journal of Ecology, 1944:		
Sales: Current vol. 32		550 7 4
Back volumes and parts		199 19 0
Reprints of Papers		38 18 6
		£789 4 10
Journal of Animal Ecology, 1944:		
Sales: Current vol. 13		223 9 2
Back volumes and parts		79 10 3
Reprints of papers		28 6 0
		331 5 5
Balance (see above, under Expenditure)		258 12 2
		£589 17 7

Expenditure

	£ s. d.	£ s. d.
Working Expenses:		
Printing and Stationery	3 18 4	
Postages	13 16 1	
Travelling	10 5 5	
Meeting Expenses	16 9 10	
Audit Fee	3 3 0	
Nature Reserves Committee, Bank Charges ...	1 2 7	
Clerical assistance	12 0 0	
		60 15 3
Grant: to Freshwater Biological Association ...		10 0 0
Biological Flora of the British Isles:		
Cost of Printing	117 2 10	
Less Sales	20 18 2	
		96 4 8
Journal of Animal Ecology. Cost *less* Sales		258 12 2
		425 12 1
Balance—Surplus for the Year (To Balance Sheet) ...		634 13 3
		£1,060 5 4
Journal of Ecology, 1944:		
Costs: Paper, Blocks, Printing and Binding ...		424 11 8
Publishers' Commission		103 3 3
Carriage, etc.		13 16 8
Insurance of Stock		6 6 11
		547 18 6
Balance (see above, under Income) ...		241 6 4
		£789 4 10
Journal of Animal Ecology, 1944:		
Costs: Paper, Blocks, Printing and Binding ...		512 5 7
Publishers' Commission		47 11 5
Carriage, etc.		10 6 6
Insurance of Stock		9 14 1
Fee for checking references		10 0 0
		£589 17 7

BALANCE SHEET AT 31 DECEMBER 1944

Assets

	£ s. d.	£ s. d.
Cash at Bank: Current Account	150 17 2	
Deposit Account	350 0 0	
		500 17 2
Publishing Accounts—Amounts due from Cambridge University Press:		
Journal of Ecology. Balance of Account	479 4 2	
Journal of Animal Ecology. Balance of Account...	161 13 11	
Journal of Ecology. Index Volume	8 1 5	
Biological Flora of the British Isles...	17 18 8	
		666 18 2
Investments at Cost:		
Held 31 December 1943—		
£1,200 of 3½ % War Loan	1,230 4 1	
£300 of 3 % Savings Bonds	300 0 0	
Purchased Jan./May 1944—		
£400 of 3 % Savings Bonds	400 0 0	
		1,930 4 1
		£3,097 19 5

A further Asset, not valued, is the Unsold Stock of Journals and Index Volume held by the Publishers for the Society.

VICTOR S. SUMMERHAYES,
ALEX. S. WATT.
Hon. Treasurers.

Liabilities

	£ s. d.	£ s. d.
Members' Subscriptions, prepaid for 1945/7... ...		19 16 9
Library Fund		1 5 0
Printing Accounts due to the Cambridge University Press:		
Journal of Ecology, vol. 32, no. 2 and Reprints ...	163 16 5	
Journal of Animal Ecology, vol. 13, no. 2 and Reprints	235 6 3	
Biological Flora, from *Journal of Ecology*, vol. 32, no. 2 & Reprints	84 12 1	
		483 14 9
General Revenue Account:		
Balance in hand 31 December 1943	1,958 9 8	
Surplus for 1944	634 13 3	
		2,593 2 11
		£3,097 19 5

Audited and found correct, and as shown by the Account Books of the Society. The Bank Balance has been verified by Bank Certificate, and also the Investments.

WM NORMAN & SONS
Chartered Accountants.

120 BISHOPSGATE, E.C. 2
and
231*a* HIGH ROAD, LOUGHTON, ESSEX.
2 *July* 1945.